

THE NAUTILUS

QL
401
.N314
I2

Volume 130, Number 2
June 15, 2016
ISSN 0028-1344

*A quarterly devoted
to malacology.*



EDITOR-IN-CHIEF

Dr. José H. Leal
The Bailey-Matthews National
Shell Museum
3075 Sanibel-Captiva Road
Sanibel, FL 33957

EDITOR EMERITUS

Dr. M. G. Harasewych
Department of Invertebrate Zoology
National Museum of
Natural History
Smithsonian Institution
Washington, DC 20560

CONSULTING EDITORS

Dr. Rüdiger Bieler
Department of Invertebrates
Field Museum of
Natural History
Chicago, IL 60605

Dr. Arthur E. Bogan
North Carolina State Museum of
Natural Sciences
Raleigh, NC 27626

Dr. Philippe Bouchet
Laboratoire de Biologie des
Invertébrés Marins et Malacologie
Muséum National d'Histoire Naturelle
55, rue Buffon
Paris, 75005 France

Dr. Robert H. Cowie
Center for Conservation Research
and Training
University of Hawaii
3050 Maile Way, Gilmore 409
Honolulu, HI 96822

Dr. Robert T. Dillon, Jr.
Department of Biology
College of Charleston
Charleston, SC 29424

Dr. Eileen H. Jokinen
8234 E. North Shore Road
Sault Ste. Marie, MI 49783

Dr. Douglas S. Jones
Florida Museum of Natural History
University of Florida
Gainesville, FL 32611-2035

Dr. Harry G. Lee
4132 Ortega Forest Drive
Jacksonville, FL 32210

Dr. Charles Lydeard
Biodiversity and Systematics
Department of Biological Sciences
University of Alabama
Tuscaloosa, AL 35487

Dr. Bruce A. Marshall
Museum of New Zealand
Te Papa Tongarewa
P.O. Box 467
Wellington, NEW ZEALAND

Dr. Paula M. Mikkelsen
Paleontological Research
Institution
1259 Trumansburg Road
Ithaca, NY 14850

Dr. Diarmaid Ó Foighil
Museum of Zoology and Department
of Biology
University of Michigan
Ann Arbor, MI 48109-1079

Dr. Gustav Paulay
Florida Museum of Natural History
University of Florida
Gainesville, FL 32611-2035

Dr. Gary Rosenberg
Department of Mollusks
The Academy of Natural Sciences
1900 Benjamin Franklin Parkway
Philadelphia, PA 19103

Dr. Ángel Valdés
Department of Malacology
Natural History Museum
of Los Angeles County
900 Exposition Boulevard
Los Angeles, CA 90007

Dr. Geerat J. Vermeij
Department of Geology
University of California at Davis
Davis, CA 95616

Dr. G. Thomas Watters
Aquatic Ecology Laboratory
1314 Kinnear Road
Columbus, OH 43212-1194

SUBSCRIPTION INFORMATION

The subscription rate for volume 130 (2016) is US \$65.00 for individuals, US \$102.00 for institutions. Postage outside the United States is an additional US \$10.00 for regular mail and US \$28.00 for air delivery. All orders should be accompanied by payment and sent to: THE NAUTILUS, P.O. Box 1580, Sanibel, FL 33957, USA, (239) 395-2233.

Change of address: Please inform the publisher of your new address at least 6 weeks in advance. All communications should include both old and new addresses (with zip codes) and state the effective date.

THE NAUTILUS (ISSN 0028-1344) is published quarterly by The Bailey-Matthews National Shell Museum, 3075 Sanibel-Captiva Road, Sanibel, FL 33957.

Periodicals postage paid at Sanibel, FL, and additional mailing offices.

POSTMASTER: Send address changes to: THE NAUTILUS
P.O. Box 1580
Sanibel, FL 33957

THE NAUTILUS

Volume 130, Number 2

June 15, 2016

ISSN 0028-1344

CONTENTS

Abraham S.H. Breure Ad Hovestadt Angela Fields David G. Robinson	The land Mollusca (Gastropoda) of Saint Kitts and Nevis (Lesser Antilles), with description of a new species 27
Vanessa Simão do Amaral Luiz Ricardo L. Simone	Comparative anatomy of five species of <i>Saccostrea</i> Dollfus and Dautzenberg, 1920 (Bivalvia: Ostreidae) from the Pacific Ocean 53
Ángel Valdés Sabrina Medrano Vishal Bhave	A new species of <i>Cuthona</i> Alder and Hancock, 1855 (Gastropoda: Heterobranchia: Nudibranchia: Tergipedidae) from the Caribbean Sea 72
Emilio F. García	The genera <i>Miraclathurella</i> Woodring, 1928 (Gastropoda: Pseudomelatomidae) and <i>Darrylia</i> García, 2008 (Gastropoda: ?Horaiclavidae), with two proposed new combinations for <i>Darrylia</i> 79

The land Mollusca (Gastropoda) of Saint Kitts and Nevis (Lesser Antilles), with description of a new species

Abraham S.H. Breure

Naturalis Biodiversity Center
P.O.Box 9517
NL-2300RA Leiden, THE NETHERLANDS
and
Royal Belgian Institute of Natural Sciences
Vautierstraat 29,
B-1000, Brussels, BELGIUM
ashbreure@gmail.com

Ad Hovestadt

Dr. Abraham Kuyperlaan 22
NL-3818JC Amersfoort, THE NETHERLANDS
ad.hovestadt@xs4all.nl

Angela Fields

Dept. Biological and Chemical Sciences
University of the West Indies
Cave Hill Campus, BARBADOS
angela.fields@cavehill.uwi.edu

David G. Robinson

USDA APHIS National Malacology Laboratory
Academy of Natural Sciences of Philadelphia
1900 Benjamin Franklin Parkway
Philadelphia, PA 19103 USA
david.g.robinson@usda.gov

ABSTRACT

An overview of the land snail fauna of the Lesser Antillean islands of Saint Kitts and Nevis is given, based on data from literature and two recent surveys. There are 33 taxa listed, of which 26 are from Saint Kitts and 22 from Nevis. One taxon is described as new: *Bulimulus ouallensis* Breure and Hovestadt. Furthermore, the following taxa are recorded from these islands for the first time: *Bulimulus diaphanus fraterculus* (Potiez and Michaud, 1835), *Obeliscus swiftianus* (Pfeiffer, 1854), and *Zonitoides arboreus* (Say, 1817). Four taxa—*Diplosolenodes* sp., *Pallifera* sp., and two *Succinea* species—could only be identified to the genus level. Three taxa, previously thought to occur on the islands, are now removed from their faunal lists, due to inaccuracies of provenance of specimens or misidentifications. Finally, remarks are given on the distribution and conservation status of species collected during the surveys.

Additional Keywords: Taxonomy, distribution, islands, West Indies

INTRODUCTION

The Reverend Smith stands in the time-honored tradition as a parson-naturalist (Armstrong, 1990). As a clergyman, he spent five years on Nevis, summarizing his findings in a 1745 book entitled: “A natural history of Nevis and the rest of the english Leeward Charibee Islands in America with many other observations on nature and art; particularly an introduction to the art of decyphering in eleven letters etc.’ He begins with observations on marine

shells, but there is no reference whatsoever to the non-marine malacofauna.

The first overview of the land shells from Saint Kitts and Nevis was published in 1862 by Thomas Bland. For Saint Christopher, the oldest English name given to the island of Saint Kitts, he listed six species in his ‘Catalogue of the Land Shells of the West Indian Islands’; Nevis was not mentioned at all. Bland (1862: 361) wrote “[t]he names of several islands do not appear in the Catalogue, because I am ignorant as to the species inhabiting them”.

The first mention of an endemic species for either Saint Kitts or Nevis was by Henry A. Pilsbry, who in 1889 described *Helix josephinae* var. *nevisensis* [now *Pleurodonte josephinae nevisensis*]; the specimen had been collected by Frederick Albion Ober. The latter being a very prolific writer and traveler, he regrettably did not mention his activities in Nevis in any detail.

William H. Rush visited Saint Kitts in 1891. His methods are still useful today: “Carriage hire was too expensive and the time at my disposal too short for any extended trip, so footing it was resorted to as the only way to reach reasonably near hunting grounds. In this manner the deep gorges up in the mountains of St. Kitts, at an elevation of one or two thousand feet were visited (. . .) Many specimens of *Bulimulus*, *Helicina* and *Amphibulima* were taken”.

Pieter Wagenaar Hummelinck visited Saint Kitts and Nevis twice, in 1949 and 1955, but apparently restricted his collecting to the coastal areas (Figure 4). His surveys provided the raw data for publications on the Vertiginidae (Haas, 1960), Subulinidae and Oleacinidae (Haas, 1962), and Bulimulidae (Breure, 1974).

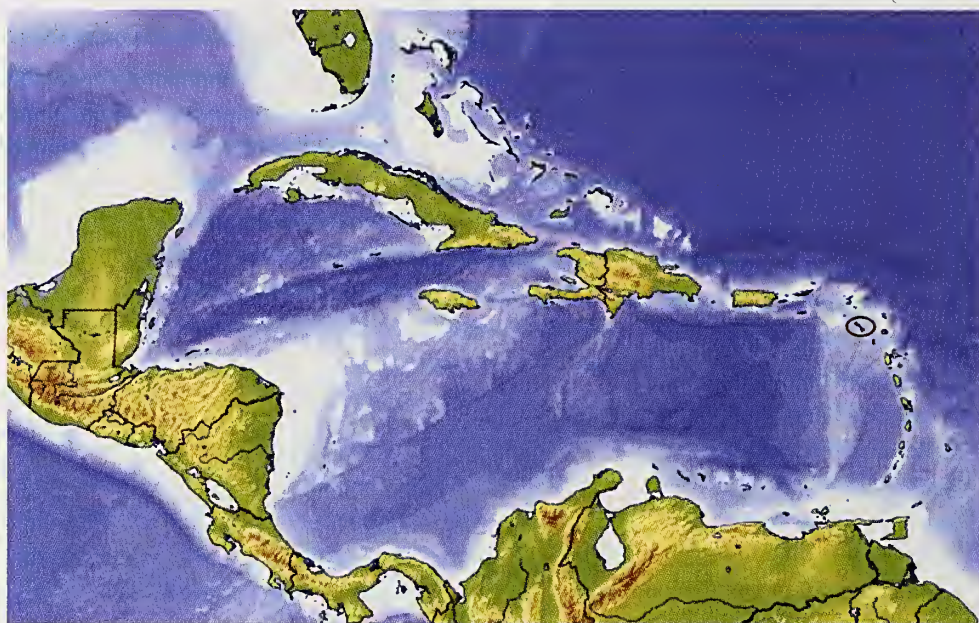


Figure 1. West Indies, showing location of Saint Kitts and Nevis (red circle). Source: Wikimedia.

Saint Kitts and Nevis is a federative, two-island state in the West Indies (Figures 1–3), and constitutes part of the British Commonwealth. The total area is 269 km², of which Saint Kitts accounts for 176 km² and Nevis 93 km².

The highest elevation on Saint Kitts is Mount Liamuiga (1156 m, also known as Mount Misery), and on Nevis it is Nevis Peak (985 m). Annual average rainfall is 1625 mm and 1170 mm respectively. On Saint Kitts, the rainfall is fairly evenly distributed over the island except for the Southeast Peninsula, which has a very dry climate.



Figure 2. Saint Kitts. Localities sampled in 2004 (yellow pins), respectively 2014 (green pins); scale = 2.5 km. Detail of area around Brimstone Hill within red quadrant; scale = 250 m. Source: Google™ Earth Pro. Image Landsat. © 2015 Google.



Figure 3. Nevis, with localities sampled in 2004 (yellow pins), respectively 2014 (green pins); scale = 1.0 km. Source: Google™ Earth Pro. Image Landsat. © 2015 Google.

From August to November there is a relatively wet season and a drier season from mid-January to April. On Nevis, rainfall is lowest on the eastern side and increases with altitude. Most rain falls between July and January (all data from Anonymous, 1991).

Geologically both islands belong to the western chain of the Lesser Antillean archipelago north of Dominica, which includes the islands of Basse Terre (Guadeloupe), Montserrat, Redonda, Nevis, Saint Kitts, Saint Eustatius, and Saba. These islands consist mostly of volcanic rocks and remain seismically active, but geological knowledge about them remains based mainly on older sources. Saint Kitts has a core of Eocene andesite, and three younger

volcanic centers which were active during the Pleistocene. Mt. Liamuiga is a stratovolcano with a deep summit crater of over 300 m diameter and, together with the other volcanic centers, are aligned along the length of the island on a NW–SE trend. A small area of Plio-Pleistocene limestone can be found at Brimstone Hill and at Godwin Chaut above 330 m (Trechmann, 1932; Martin-Kaye, 1959; Westermann and Kiel, 1961; Anonymous, 1991; Toothill et al., 2007). The oldest rocks of Nevis are of marine origin, but the island is comprised mainly of dacites, with andesites in a number of places. Limestone can be found on the southern slopes of Saddle Hill (Westermann and Kiel, 1961; Hutton, 1968; Hutton and Nockolds, 1978).

Table 1. Localities mentioned in this paper.

Island	Locality	Alt.	1949	2004	2014	LAT	LON
STK	St. George, Basseterre, La Guérite	50	419	01		17.299472	−62.732917
	St. Thomas, midway up Brimstone Hill	175		02		17.34625	−62.836056
	St. Thomas, lower slope of Brimstone Hill	129		03		17.348306	−62.837639
	St. Thomas, base of Brimstone Hill	47		04		17.348194	−62.840583
	St. Paul, crater trail up Mt. Liamuiga	327		05		17.382694	−62.826806
	St. Thomas, trail to D'O's Dane Pond	556		06		17.345	−62.790417
	Christchurch, trail to Phillips Level	438		07A		17.352944	−62.774111
	Christchurch, trail from Phillips to Phillips Level	463		07B		17.346278	−62.780806
	Trinity, Mattingly Flower Farm	66		08		17.29725	−62.752028
	St. George, road to Turtle Beach, south of Salt Pan	39		09		17.236306	−62.640556
	St. George, Friars Beach Bay	8		10		17.276861	−62.674139
	St. George, road south of Basseterre	79		11		17.280583	−62.678722
	St. Thomas, railway cut at base Brimstone Hill	44		12		17.34375	−62.838278
	Trinity, top of Ottley's Level	490		21		17.310611	−62.768556
	Trinity, base of Ottley's Level	290		22		17.307139	−62.766222
	St. John, Lavington Ghut	189		23		17.391	−62.797861
	North Frigate Bay, Sugar Bay Club	11			2	17.286972	−62.685083
	Romney Manor	61			3	17.326833	−62.800806
	St. Thomas, Brimstone Hill, near barracks	221	421		4	17.347806	−62.835
	St. Thomas, NW side Brimstone Hill	78	422		5	17.348583	−62.840194
	Trinity, Ottley Plantation House	155			6	17.357028	−62.7475
	Trinity, along track to Ottley Level	342			7	17.310389	−62.765444
	St. Pauls, trailhead to Liamuiga	257			8	17.382861	−62.832556
	St. George, E Basseterre, Mome Hills	45	417			17.297564	−62.699269
	Wingfield River, 300 m N bridge	50 ²	420			17.322917	−62.802783
NEV	St. John, Montpellier Estate, botanical garden	190		13		17.123028	−62.594056
	St. George, Golden Rock	294		14		17.145306	−62.567306
	St. George, Frenchman's Cave	164		15		17.150083	−62.557611
	St. John, Experimental Station, greenhouse	80		16		17.125556	−62.608972
	St. James, above Prison Farm, cloud forest	269		17		17.165611	−62.571
	St. James, above Prison Farm, cloud forest	188			10	17.169389	−62.563611
	St. James, above Prison Farm, cloud forest	255			11	17.166444	−62.57025
	St. James, Camp's River	69		18		17.189361	−62.578472
	St. James, Spring Hill, stunted forest	231		19		17.174667	−62.592694
	St. Thomas, Westbury, greenhouse	17		20		17.184028	−62.617083
	Herbert Heights, trail up Nevis Peak	367		24a		17.141806	−62.576528
	Herbert Heights, trail up Nevis Peak	467		24b		17.141306	−62.583278
	St. George, surroundings of Peak Heaven	466			9	17.141528	−62.583389
	Saddle Hill	364			12	17.118861	−62.577139
	Hamilton Estate ruins	153			13	17.138889	−62.607194
	St. George, N of Golden Rock Inn, along Source trail	445			14	17.153139	−62.571167
	Montraves Estate	103			15	17.152528	−62.612889
	West of Jessops Village	1	414			17.164553	−62.628825
	Near Mosquito Bay	30	415			17.202333	−62.609386
	Jones River, E of Newcastle	15 ²	416			17.200728	−62.578408

Vegetation types occurring on the two islands have been extensively described by Lindsay and Horwith (1999) based on a modification of Beard (1949). Helmer et al. (2008) compared the data from Beard (1949) with recent data and calculated the change in land cover data based on satellite imagery.

The aim of this paper is to present the combined results of two malacological surveys, respectively conducted in 2004 (by D.G. Robinson and collaborators) and 2014 (by A. Hovestadt), and to summarize the malacofauna of these islands.

MATERIALS AND METHODS

Both above-mentioned, recent surveys yielded data on 40 localities in total. Localities are presented with their coordinates as they were recorded by D.G. Robinson and collaborators (field work during 2004) and A. Hovestadt (field work during 2014) respectively (Table 1). Altitudes for the former have been taken from Google Earth v.7.1.2.2041. Coordinates of these localities were plotted in SimpleMappr (Shorthouse, 2010) and exported as KML file. For historical comparisons, the localities sampled by P. Wagenaar Hummelinck (1949) have been added in Table 1; coordinates of these (estimated from Google Earth) are based on his map (Figure 4; Wagenaar Hummelinck, 1953: 20–21, Figure 19), and are less precise than the recent ones. The species occurrence data for these localities are only partial (Haas 1960, 1962; Breure, 1974).

The above genus-levels taxonomy follows Bouchet et al. (2005). Under each species, references are made only to the literature including records from Saint Kitts and Nevis.

The diversity of sampled localities was analyzed to determine “hotspots” of land snail diversity on the two

islands, following the same method as applied by Robinson et al. (2009) for Dominica. When more species are present in a given locality, also rare species will be better represented. Therefore, each occurrence was given a “rareness factor” ($R = 1/L$; L equals the number of localities where a species is present). R varies in this study from 0.025 (the species occurs at all 40 localities where molluscs have been collected) to 1.000 (the species occurs at a single locality only). Finally, the diversity per locality is calculated, both as total and for endemic species only ($D_{\text{tot}} = \sum R_{\text{tot}}/S$; $D_{\text{end}} = \sum R_{\text{end}}/S$; S , species richness as the number of species per locality). Localities sampled by Wagenaar Hummelinck, with partial species occurrence data, have been excluded from these calculations.

Abbreviations for depository collections are: AH, collection of A. Hovestadt, Amersfoort, the Netherlands; ANSP, Academy of Natural Sciences of Philadelphia, Philadelphia, USA; FMNH, Field Museum of Natural History, Chicago, USA; RMNH, Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie), Leiden, the Netherlands; SMF, Senckenberg Natur-Museum, Frankfurt am Main, Germany; UF, Florida State Museum of Natural History, Gainesville, U.S.A.; USDA, United States Department of Agriculture, Animal and Plant Health National Malacology Collection, ANSP, Philadelphia, USA. Other abbreviations are: leg., for “collected by,” and “coll.” for “Collection.” An asterisk (*) indicates an observation only, material not collected.

SYSTEMATICS

Superfamily Helicinoidea *sensu* Thompson, 1980
Family Helicinidae Férussac, 1822

Genus *Helicina* Lamarck, 1799

Helicina fasciata Lamarck, 1822
(Figures 20, 22–23)

Helicina fasciata Lamarck, 1822.—Bland, 1862: 358 (St. Christopher); Clench, 1956: 69 (St. Kitts, Nevis).

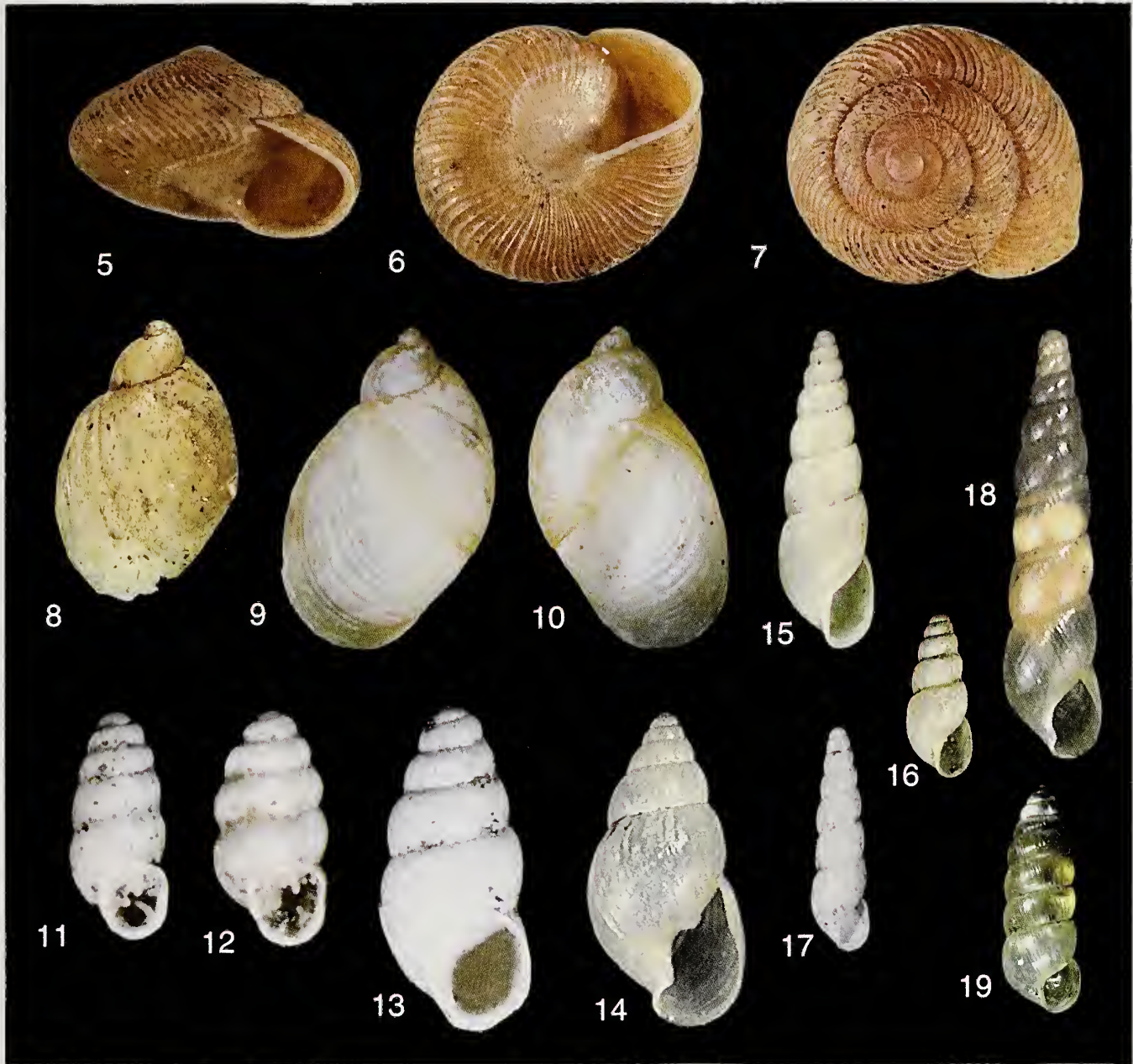
Survey Material: **ST. KITTS:** Christchurch, Nichola Town Parish, trail to Phillips Level, (USDA); St. Thomas, Middle Island Parish, trail to D’Os Dane Pond (USDA); Trinity, Palmetto Point Parish, top of Ottley’s Level (USDA); *ibid.*, near base of Ottley’s Level (USDA); **NEVIS:** St. George, Gingerland Parish, Golden Rock (AH; USDA); *ibid.*, Herbert Heights, trail to Nevis Peak (USDA); *ibid.*, near Peak Heaven (AH); St. James, Windward Parish, above Prison Farm, cloud forest (AH; USDA).

Additional Material Examined: **ST. KITTS:** ex Swift coll. (ANSP 14914); W.H. Rush leg., 1891 (ANSP 62064). **NEVIS:** C.A. Barber leg. (ANSP 78304); *ibid.*, J. Bond leg., 1929 (ANSP 149430).

Distribution: Lesser Antilles, where it is widespread as a result of human activities.



Figure 4. Saint Kitts and Nevis, localities sampled in 1949 (Wagenaar Hummelinck, 1953: fig. 16).



Figures 5–19 Helicinidae, Succineidae, Vertiginidae, and Subulinidae species. **5–7.** *Lucidella* (*Poeniella*) *plicatula christophori* (Pilsbry, 1897), H = 4.2 mm. **8.** *Succinea* species A, H = 9.3 mm. **9–10.** *Succinea* species B, H = 11.3 mm. **11.** *Gastrocopta rupicola marginalba* (L. Pfeiffer, 1840), H = 2.2 mm. **12.** *Gastrocopta servilis* (Gould, 1843), H = 2.3 mm. **13.** *Pupoides marginatus nitidulus* (L. Pfeiffer, 1839), H = 3.6 mm. **14.** *Leptinaria unilamellata* (d'Orbigny, 1837), H = 10.6 mm. **15.** *Allopeas gracile* (Hutton, 1834), H = 7.0 mm. **16.** *Allopeas micra* (d'Orbigny, 1835), H = 6.0 mm. **17.** *Obeliscus swiftianus* (L. Pfeiffer, 1854), H = 7.2 mm. **18.** *Subulina octona* (Bruguière, 1789), H = 19.7 mm. **19.** *Beckianum beckianum* (L. Pfeiffer, 1846), H = 6.9 mm.

Habitat: Occurs in a wide range of habitats, from relatively undisturbed (cloud forest) to disturbed (area with *Heliconia* plants).

Remarks: This species exhibits a marked preference for humid conditions in dense vegetation (e.g., humid scrub forest, cloud forest), being particularly abundant on the upper slopes of Nevis Peak. It shows a high variety of colors, even in specimens within the same population.

Genus *Lucidella* Swainson, 1840

Subgenus *Poeniella* H.B. Baker, 1923

Lucidella (*Poeniella*) *plicatula christophori* (Pilsbry, 1897)
(Figures 5–7, 21)

Helicina plicatula var. *christophori* Pilsbry, 1897: 118
(Type locality: St. Kitts).



Figures 20–21. Distribution of Helicinidae. **20.** *Helicina fasciata* Lamarck, 1822 (red star). **21.** *Lucidella (Poenilla) plicatula christophori* (Pilsbry, 1897) (blue triangle).

Helicina christophori Pilsbry, 1897.—H.B. Baker, 1923: 23.

Lucidella plicatula christophori (Pilsbry, 1897).—Boss and Jacobson, 1974: 31.

Survey Material: **ST. KITTS:** Trinity, Palmetto Point Parish, top of Ottley's Level (USDA); *ibid.*, near base of Ottley's Level (USDA); **NEVIS:** St. James, Windward Parish, above Prison Farm, cloud forest (USDA); *ibid.*, Camp's River (USDA); St. George, Gingerland Parish, Saddle Hill (AH).

Additional Material Examined: **ST. KITTS:** W.H. Rush leg. (ANSP 62062, lectotype); *ibid.* (ANSP 358494, paralectotypes).

Distribution: Saint Kitts, Nevis.

Habitat: It is believed to live in damp leaf litter and under rotting logs.

Remarks: This species appears to be relatively rare, as we found only empty shells.

Superfamily Veronicelloidea Gray, 1840
Family Veronicellidae Gray, 1840

Genus *Diplosolenodes* Thomé, 1975

***Diplosolenodes* species**

(Figure 27, 31)

Survey Material: **NEVIS:** St. George, Gingerland Parish, Herbert Heights, trail to Nevis Peak (USDA).

Remarks: There is insufficient material to determine if this is a more widespread species occurring on other Antillean islands.

Genus *Veronicella* de Blainville, 1817

***Veronicella cubensis* (L. Pfeiffer, 1840)**
(Figures 26, 31)

Survey Material: **SAINT KITTS:** St. Thomas, Middle Island Parish, fortifications midway up Brimstone Hill (USDA); Trinity, Palmetto Point Parish, Ottley Plantation House (AH*); **NEVIS:** St. George, Gingerland Parish, Golden Rock (USDA).

Distribution: Cuba, Hispaniola, Puerto Rico, Antigua, Saint Kitts, Nevis, Dominica, Barbados. Introduced to various Pacific islands (Hawaiian Islands, Guam, northern Marianas).

Remarks: Robinson et al. (2009) mentioned this species from Saint Kitts and Nevis, without providing further evidence. Although it has been reported as a serious agricultural pest (especially on Pacific islands), this species is of no such concern at the moment on these two islands.

***Veronicella aff. floridana* (Leidy in Binney, 1851)**
(Figures 25, 31)

Survey Material: **SAINT KITTS:** Trinity, Palmetto Point Parish, nursery of Mattingly Flower Farm (USDA); *ibid.*, top of Ottley's Level (USDA); **NEVIS:** St. John, Figtree Parish, Montpellier Estate, botanical garden (USDA).

Distribution: Florida, throughout the West Indies.

Remarks: This invasive slug species is here reported from Saint Kitts and Nevis for the first time. It has become an agricultural pest in other parts of the West Indies, where it feeds on a wide range of species. Dissection is required to accurately identify this and the previous species, as the two can bear some morphological similarity.

Superfamily Succineoidea Beck, 1837

Family Succineidae Beck, 1837



Figures 22–30. Living snails of the families Helicinidae, Philomycidae, Veronicellidae, Streptaxidae, Subulinidae, and Pleurodontidae. **22–23.** *Helicina fasciata* Lamarck, 1822. **24.** *Pallifera* species. **25.** *Veronicella* aff. *floridana* (Leidy in Binney, 1851). **26.** *Veronicella cubensis* (L. Pfeiffer, 1840). **27.** *Diplosenodes* species. **28.** *Streptartemon glaber* (L. Pfeiffer, 1849). **29.** *Subulina octona* (Bruguière, 1789). **30.** *Pleurodonte josephinae nevisensis* (Pilsbry, 1889).

Genus *Succinea* Draparnaud, 1801

Succinea species A (Figures 8, 32)

Survey Material: SAINT KITTS: St. George, Basseterre, road south of Basseterre (USDA).

Remarks: The taxonomy of West Indian succinids is poorly understood, and a revision is long overdue. Not many anatomical or molecular studies have been made on this group, and various names have been used indiscriminately by malacological workers over the centuries for snails on different Antillean islands.

Succinea species B (Figures 9, 10, 32)

Material Examined: NEVIS: St. John, Figtree Parish, Prospect, greenhouse of Experimental Station (USDA);

St. Thomas Lowland, greenhouse of Taiwanese technical Mission (USDA).

Distribution: Florida, Puerto Rico, Nevis.

Remarks: This species was likely introduced with horticultural imports from southern Florida or from Puerto Rico, as it closely resembles material found in greenhouses in those areas.

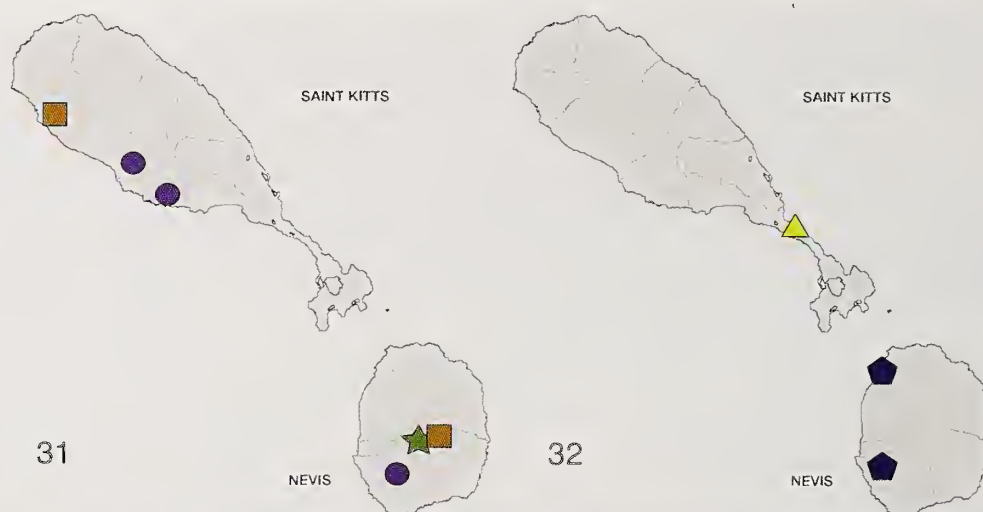
Superfamily Achatinoidea Swainson, 1840

Family Subulinidae P. Fischer and Crosse, 1877

Genus *Allopeas* H.B. Baker, 1935

Allopeas gracile (Hutton, 1834) (Figures 15, 33)

Lamellaxis (Allopeas) gracile (Hutton [1834]).—Haas, 1962: 56; St. Christopher, Brimstone Hill; Nevis: Jessops Village.



Figures 31–32. Distribution of Veronicellidae and Succineidae. **31.** *Diplosolenodes* sp. (green star), *Veronicella cubensis* (L. Pfeiffer, 1840) (orange rectangle), and *Veronicella* aff. *floridensis* (Leidy in Binney, 1851) (purple circle). **32.** *Succinea* sp. A (yellow triangle), *Succinea* sp. B (dark blue polygon).

Survey Material: **SAINT KITTS:** St. George, Basseterre Parish, Basseterre, La Guerite, Department of Agriculture (USDA); *ibid.*, road south of Basseterre (USDA); St. Thomas, Middle Island Parish, base of Brimstone Hill (USDA); *ibid.*, near barracks (AH); **NEVIS:** St. George, Gingerland Parish, Saddle Hill (AH); *ibid.*, Montravers Estate (AH); St. John, Figtree Parish, Montpellier Estate, botanical garden (USDA).

Distribution: West Indies, southern Mexico, Central and South America; distributed throughout the subtropics worldwide.

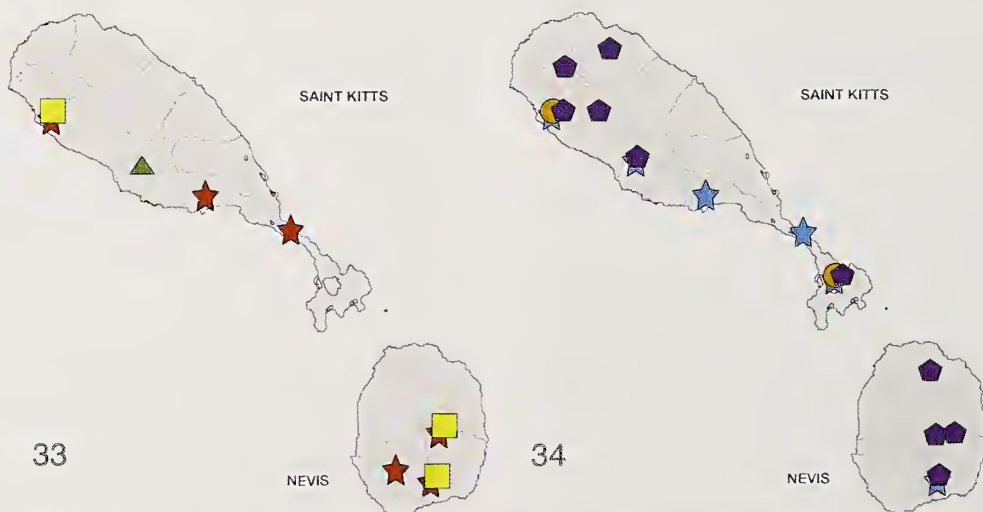
Allopeas micra (d'Orbigny, 1835)
(Figures 16, 34)

Lamellaxis (Allopeas) micron (d'Orbigny, [1835]).—
Haas, 1962: 57; St. Christopher, Brimstone Hill;
Morne Hills.

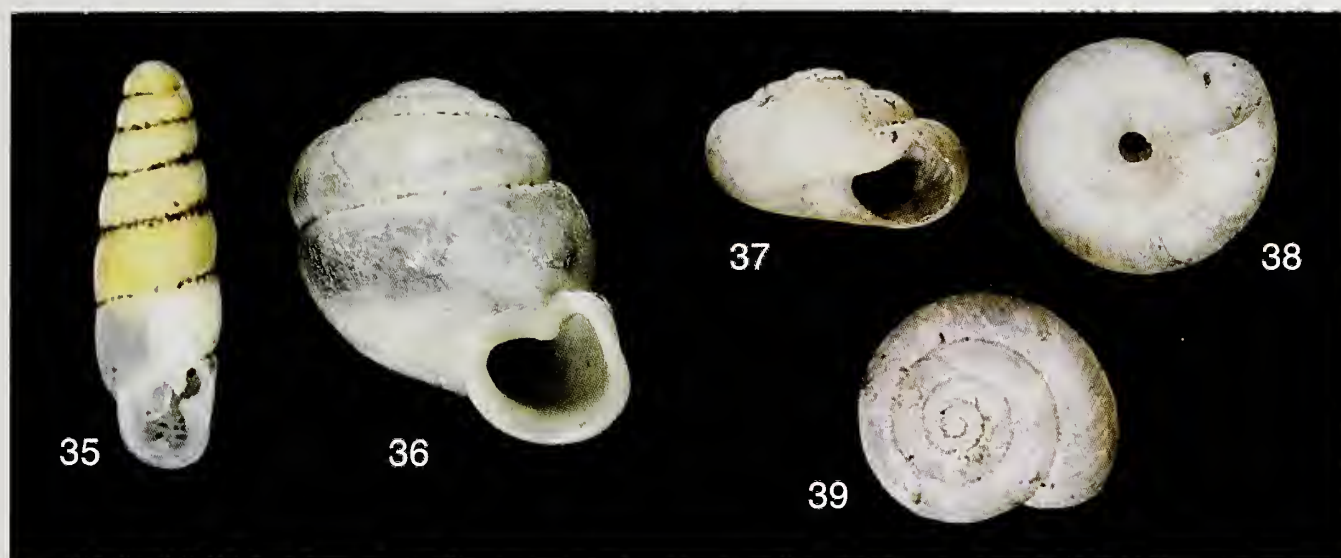
Survey Material: **SAINT KITTS:** St. George, Basseterre Parish, Basseterre, La Guerite, Department of Agriculture (USDA); *ibid.*, road to Turtle Bay, south of Salt Pan (USDA); *ibid.*, road south of Basseterre (USDA); St. Thomas, Middle Island Parish, lower slope of Brimstone Hill (USDA); *ibid.*, NW-side Brimstone Hill (AH); Trinity, Palmetto Point Parish, near base of Ottley's Level (USDA); **NEVIS:** St. George, Gingerland Parish, Saddle Hill (AH).

Distribution: West Indies, Mexico to Bolivia.

Remarks: The specimens found are up to 6 mm in height.



Figures 33–34. Distribution of Subulinidae. **33.** *Allopeas gracile* (Hutton, 1834) (red star), *Beckianum beckianum* (L. Pfeiffer, 1846) (yellow rectangle), *Leptinaria unilamellata* (d'Orbigny, 1837) (green triangle). **34.** *Allopeas micra* (d'Orbigny, 1835) (light blue star), *Obeliscus swiftianus* (L. Pfeiffer, 1853) (orange circle), *Subulina octona* (Bruguère, 1789) (purple polygon).



Figures 35–39. Streptaxidae and Sagdidae species. **35.** *Huttonella bicolor* (Hutton, 1834), H = 6.0 mm. **36.** *Streptartemon glaber* (L. Pfeiffer, 1849), H 6.8 mm. **37–39.** *Hojeda* species, D = 4.5 mm.

Genus *Beckianum* H.B. Baker, 1961

Beckianum beckianum (L. Pfeiffer, 1846)
(Figure 19, 33)

Diaopeas beakianum (L. Pfeiffer [, 1846]).—Haas, 1962: 55. St. Christopher, La Guérite; Nevis, near Jessops Village.

Survey Material: **SAINT KITTS:** St. Thomas, Middle Island Parish, lower slope of Brimstone Hill (USDA); *ibid.* base of Brimstone Hill (USDA); *ibid.*, near barracks and on NW side of Brimstone Hill (AH); **NEVIS:** St. George, Gingerland Parish, Montraves Estate (AH); St. John, Figtrees Parish, Saddle Hill (AH).

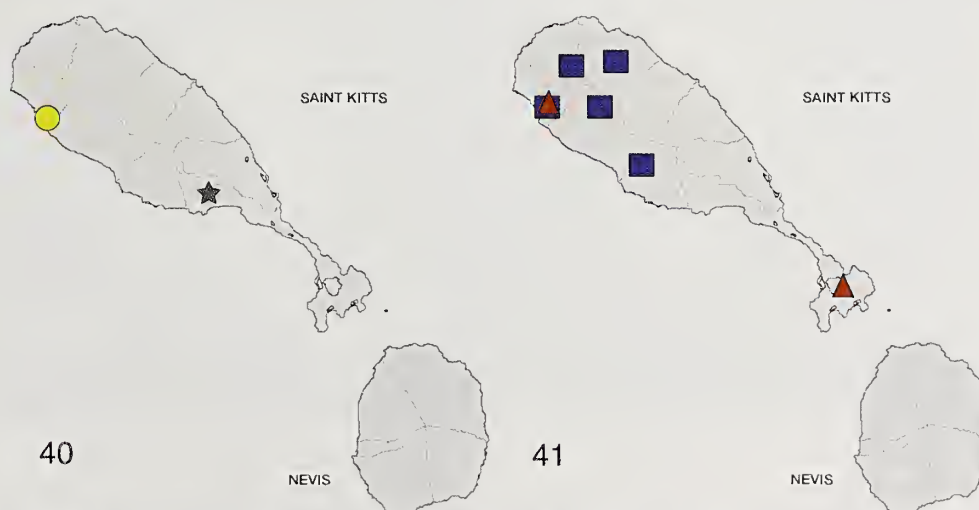
Distribution: West Indies, Central America.

Remarks: Material collected was up to 9 mm in height. This is the first report of this taxon from Nevis.

Genus *Leptinaria* Beck, 1837

Leptinaria unilamellata (d'Orbigny, 1837)
(Figures 14, 33)

Survey Material: **SAINT KITTS:** Trinity, Palmetto Point Parish, top of Ottley's Level (USDA). **NEVIS:** St. George, Gingerland Parish, Golden Rock (USDA); *ibid.*, Frenchman's Cave (USDA); Herbert Heights, trail to Nevis Peak (USDA).



Figures 40–41. Distribution of Streptaxidae and Gastrocoptidae. **40.** *Huttonella bicolor* (Hutton, 1834) (grey star), *Gastrocopta rupicola marginalba* (L. Pfeiffer, 1840) (yellow circle). **41.** *Streptartemon glaber* (L. Pfeiffer, 1849) (blue rectangle), *Gastrocopta servilis* (Gould, 1843) (red triangle).

Distribution: West Indies, Central America to Venezuela and Peru.

Habitat: Generally found in damp leaf litter and under rotting logs.

Remarks: The specimens collected obtain a maximum shell height of 15 mm. This species is particularly abundant in disturbed habitats, especially in agricultural areas.

Genus *Obeliscus* Beck, 1837

Subgenus *Stenogyra* Shuttleworth, 1854

***Obeliscus (Stenogyra) swiftianus* (L. Pfeiffer, 1853)**
(Figures 17, 34)

Opeas octogyrum plicatellum (Guppy [, 1868]).—Haas, 1962: 55; St. Christopher, Brimstone Hill.

Survey Material: **SAINT KITTS:** St. George Basseterre Parish, road to Turtle Bay, south of Salt Pan (USDA); St. Thomas Middle Island Parish, lower slope of Brimstone Hill (USDA).

Distribution: Puerto Rico and northeastern Lesser Antilles.

Remarks: Haas (1962) misidentified this snail, using the name of a related species from Trinidad; we believe that his illustrated species is *Allopeas gracile*. This is the first confirmed record for Saint Kitts.

Genus *Subulina* Beck, 1837

***Subulina octona* (Bruguière, 1789)**
(Figures 18, 29, 34)

Subulina octona (Bruguière [, 1789]).—Haas, 1962: 49. St. Christopher, Winfield River; Brimstone Hill; Timothy Hill at Frigate Bay; Nevis, Jessops Village, Nelson's Spring, Jones' River.

Survey Material: **SAINT KITTS:** St. George, Basseterre Parish, road to Turtle Bay, south of Salt Pan (USDA); St. John, Capisterre Parish, Saddler's Land Settlement, Lavington Ghut (USDA); St. Paul, Capisterre Parish, trailhead to Mount Liamuiga (AH); St. Thomas, Middle Island Parish, lower slope of Brimstone Hill (USDA); *ibid.*, trail to D'O's Dane Pond, off Old Military trail (USDA); Trinity, Palmetto Point Parish, top of Ottley's Level (USDA); *ibid.*, near base of Ottley's Level (USDA); **NEVIS:** St. George, Gingerland Parish, along Source trail, N of Golden Rock Inn (AH); St. John, Figtree Parish, Saddle Hill (AH).

Distribution: Worldwide tropics and subtropics; in temperate zones in greenhouses.

Remarks: This widely distributed species, probably introduced centuries ago from Africa, is now one of the commonest species in the tropics and subtropics. It is

considered to be an indicator of disturbed environments. The species is now recorded for the first time from Nevis.

Superfamily Streptaxoidea Gray, 1860

Family Streptaxidae Gray, 1860

Genus *Streptartemon* Kobelt, 1905

***Streptartemon glaber* (L. Pfeiffer, 1849)**
(Figures 28, 36, 41)

Material: **SAINT KITTS:** St. George, Basseterre Parish, road to Turtle Bay, south of Salt Pan (USDA); St. John, Capisterre Parish, crater trail up Mount Liamuiga (USDA); St. Thomas, Middle Island Parish, lower slope of Brimstone Hill (USDA); *ibid.*, near barracks and NW side of Brimstone Hill (AH); *ibid.*, trail to D'O's Dane Pond, off Old Military trail (USDA); Trinity, Palmetto Point Parish, top of Ottley's Level (USDA); *ibid.*, near base of Ottley's Level (USDA).

Distribution: Puerto Rico, U.S. Virgin Islands, Saint Thomas, Saint Croix, Saint Kitts, Dominica, Barbados, Venezuela, Guyana, Surinam, Brazil.

Remarks: This South American carnivorous species has been introduced throughout the Lesser Antilles by human activity. It appears to be very widespread on Saint Kitts; its effect on the native mollusks remains undocumented as yet.

Genus *Huttonella* L. Pfeiffer, 1856

***Huttonella bicolor* (Hutton, 1834)**
(Figures 35, 40)

Ennea (Huttonella) bicolor Hutton, 1834.—Tryon, 1885: 104; introduced to West Indies [no records for Saint Kitts and Nevis].

Survey Material: **SAINT KITTS:** St. George, Basseterre Parish, Basseterre, La Guerite, Department of Agriculture (USDA).

Distribution: Africa; introduced into the tropics and subtropics worldwide, including USA (Florida), West Indies, Panama, Brazil.

Remarks: Specimens of this carnivorous species found on Saint Kitts have a shell height of up to 6.75 mm. The species might have been imported with potted plants. This is the first record for this island.

Superfamily Gastrodontoidea Tryon, 1866

Family Gastrodontidae Tryon, 1866

Genus *Zonitoides* Lehmann, 1862

***Zonitoides arboreus* (Say, 1817)**

Survey Material: **SAINT KITTS:** Saint Thomas, Middle Island Parish, NW side of Brimstone Hill (AH).



Figures 42–51. Amphibulimidae and Bulimulidae species. **42–43.** *Amphibulima patula christopheri* Pilsbry, 1902, H = 17.3 mm. **44–45.** *Drymaeus (Antidrymaeus) multifasciatus christopheri* Pilsbry, 1899, H = 16.4 mm, respectively H = 14.6 mm. **46.** *Drymaeus (Antidrymaeus) multifasciatus* subspecies, H = 16.2 mm. **47.** *Bulimulus gittenbergeri* Breure, 1974, holotype RMNH 54903, H = 20.7. **48–49.** *Bulimulus guadalupensis* (Bruguière, 1789), H 17.6 mm, respectively H 17.4 mm. **50.** *Bulimulus ouallensis* Breure and Hovestadt new species, holotype RMNH 5003990, H = 19.0. **51.** *Bulimulus diaphanus fraterculus* (Potiez and Michaud, 1835), H = 16.5 mm.

Table 2. *Bulimulus ouallensis* Breure and Hovestadt new species. Measurements of the type material. Abbreviations: D, diameter; H, shell height; HA, height of aperture; LW, height of last whorl; P, number of protoconch whorls; W, total number of whorls; WA, width of aperture (all in mm). See also Breure (1974: figs 2–5).

	H	D	HA	WA	LW	W
Holotype	19	8.9	8.4	4.5	13	6.5
Paratype	20	8.5	8.8	5.5	14.3	6.5
Paratype	16.3	8.3	7.5	4.6	11.2	6
Paratype	19	9.4	6.8	4.8	10.9	6.3

Distribution: Widespread in North America, Bahamas, Puerto Rico.

Remarks: This is the first record for Saint Kitts of this widespread species, which is likely to have been introduced.

Superfamily Orthalicoidae Albers, 1860

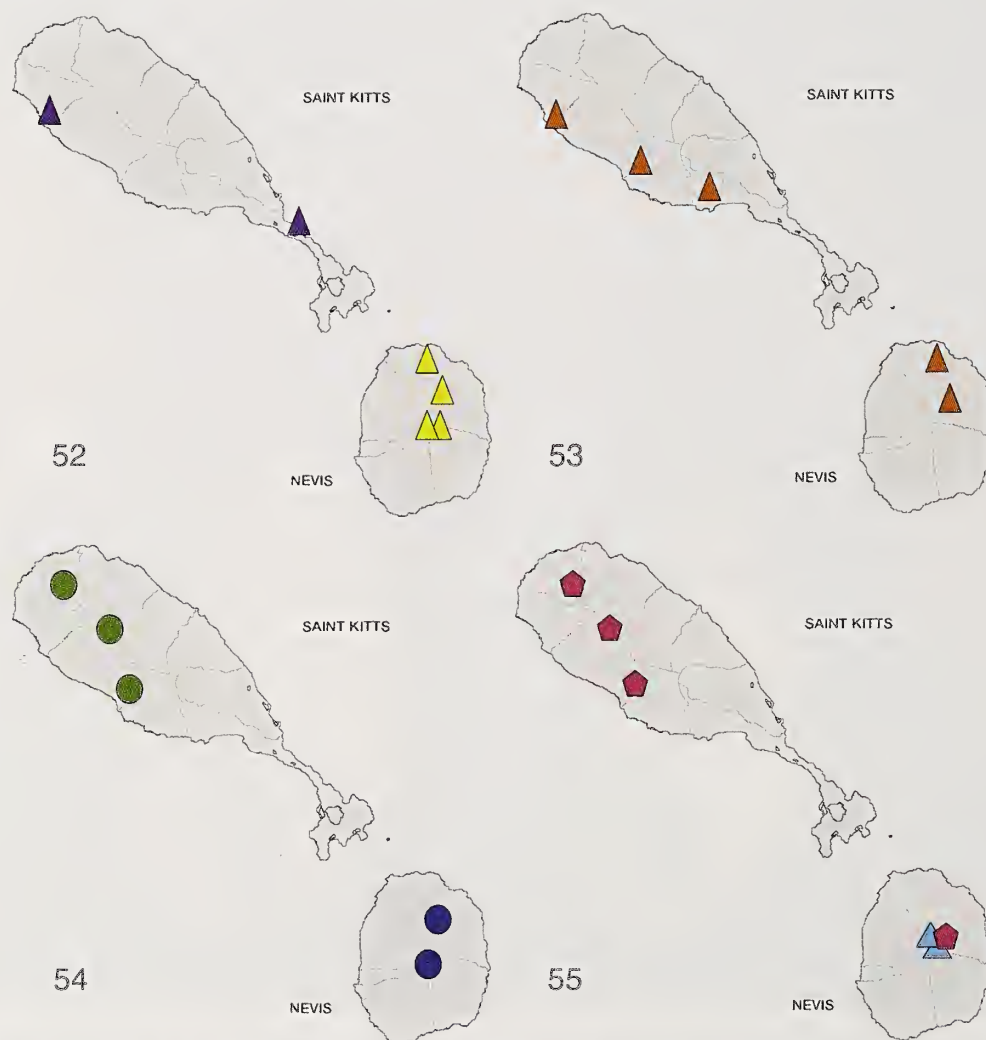
Family Bulimulidae Tryon, 1867

Genus *Bulimulus* Leach, 1814

Remarks: The species of this genus are usually difficult to differentiate, most of them being brownish and of similar shape. The accurate identification of several species from these islands can only be achieved through careful comparisons.

Bulimulus diaphanus fraterculus (Potiez and Michaud, 1835)
(Figures 51–52)

Bulimulus fraterculus 'F[érussac]' Potiez and Michaud, 1835.—Bland, 1862: 358; St. Kitts.



Figures 52–55. Distribution of Bulimulidae and Amphibulimidae. 52. *Bulimulus gittenbergeri* Breure, 1974 (purple triangle), *B. diaphanus fraterculus* (Potiez and Michaud, 1835) (yellow triangle). 53. *Bulimulus guadalupensis* (Bruguère, 1789) (orange triangle). 54. *Drymaeus multifasciatus christopheri* Pilsbry, 1899 (green circle), *D. multifasciatus* subspecies (dark blue circle). 55. *Bulimulus ouallensis* Breure and Hovestadt new species (light blue triangle), *Amphibulima patula christopheri* Pilsbry, 1902 (dark red polygon).

Bulimulus fraterculus Potiez and Michaud, 1835.—Pilsbry, 1897 [1897–1898]: 46, pl. 11 figs 24–25 (excluding Bland's record).

Bulimulus diaphanus fraterculus Potiez and Michaud, 1835.—Breure, 1974: 32, pl. 3 figs 6–10; pl. 7 fig. 1; reference to Bland's record.

Survey Material: NEVIS: St. John, Windward Parish, cloud forest above Prison Farm (AH).

Distribution: Saint Martin, Saint Barts, Saba, Saint Eustatius, Nevis, Barbuda, Antigua, Guadeloupe, Les Saintes, Dominica.

Remarks: This taxon has been mentioned from Saint Kitts by Bland (1862), but no voucher material could be traced by Breure (1974). Pilsbry (1897 [1897–1898]: 46) wrote: “The *B. fraterculus* of American collections, reported from Porto Rico, St. Kitts, St. Croix, Antigua, St. John, St. Thomas, Trinidad and Barbados, is not this species; so the localities cited by Pfr. in Monogr. viii, p. 189, and by Smith, Ann. Mag. (6), viii, on the authority of Bland, do not refer to the true *fraterculus*”. Breure (1974), after having found type material of Potiez and Michaud at the Muséum National d'Histoire Naturelle, Paris, confirmed the presence of this taxon only on the islands of Saint Martin, Saba, Saint Eustatius, Barbuda, and Guadeloupe. This is the first record for Nevis.

***Bulimulus guadalupensis* (Bruguère, 1789)**
(Figures 48–49, 53)

Bulimus exilis Gmelin, 1791.—Bland, 1862: 358; St. Kitts.

Bulimulus exiles [sic] Gmelin, 1791.—Rush, 1891: 69.

Bulimulus exilis Gmelin, 1791: Pilsbry, 1897 [1897–1898]: 37, pl. 9 figs 61–67; St. Christopher or St. Kitts.

Bulimulus (*Bulimulus*) *guadalupensis* (Bruguère, 1789).—Breure, 1974: 15, figs 6–60, pl. 2.; St. Kitts, Timothy Hill at Frigate Bay; Frigate Bay beach; between Jugate Bay and Basseterre; Phillips. Nevis.

Survey Material: SAINT KITTS: St. George, Basseterre Parish, Basseterre, La Guerite, Department of Agriculture (USDA); St. Thomas, Middle Island Parish, lower slope of Brimstone Hill (USDA); Trinity, Palmetto Point Parish, top of Ottley's Level (USDA); *ibid.*, near base of Ottley's Level (USDA); NEVIS: St. James, Windward Parish, above Prison Farm (USDA); *ibid.*, Camp's River (USDA).

Additional Material Examined: SAINT KITTS: T. Bland leg., ex A.D. Brown (ANSP 3519); Dietz leg., ex Swift coll. (ANSP 25574); C.A. Barber leg., ex T.D.A. Cockerell (ANSP 78301).

Distribution: Probably originated in the Windward Islands (Breure, 1974); now distributed throughout the Caribbean Basin, including Florida.

***Bulimulus gittenbergeri* Breure, 1974**
(Figures 47, 52)

Bulimulus gittenbergeri Breure, 1974.—27, pl. 5 figs 10–13; pl. 7 figs 3; St. Kitts, limestone NW Brimstone Hill.

Survey Material: SAINT KITTS: St. George, Basseterre Parish, road south of Basseterre (USDA); St. Thomas, Middle Island Parish, lower slope of Brimstone Hill (USDA); *ibid.*, Brimstone Hill (AH).

Additional Material Examined: SAINT KITTS: NW Brimstone Hill (RMNH 54903, holotype), RMNH 54904, FMNH 174171, SMF 225900 (paratypes); top of Brimstone Hill (RMNH), Wingfield River (RMNH).

Distribution: Endemic to Saint Kitts.

Habitat: Occurring in arid scrub forests of the coastal zone, where it was collected among shrubs.

Remarks: The specimens collected have a shell height up to 20.5 mm.

***Bulimulus ouallensis* Breure and Hovestadt new species**
(Figures 50, 55)

Diagnosis: A species of *Bulimulus* up to 20.0 mm, with slightly convex sides and a rather thin shell, sculptured with spiral striation on the epidermis, protoconch pit-reticulated in its latter half.

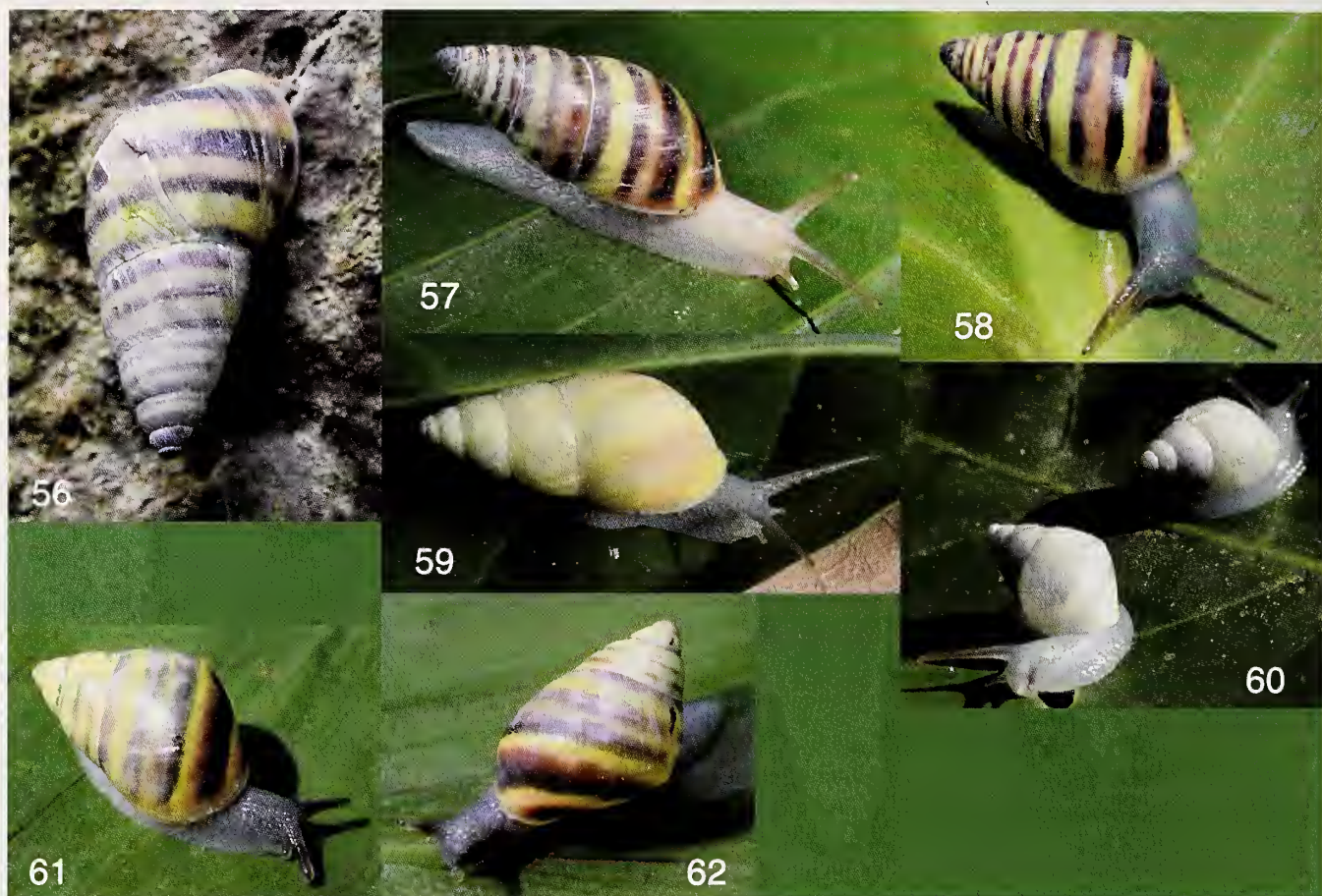
Description: Shell up to 20.0 mm, 2.1 times as long as wide; narrowly perforated, acute with slightly convex sides; rather thin. Colour light brown when epidermis present, apex purplish-brown. Surface opaque, epidermis usually with very delicate spiral striae; teleoconch sculptured with incrassate growth striae, approximately 1 mm apart; striae fuse into white tufts, giving the impression of a narrow white band running just below suture. Protoconch marked with oblique riblets running at an angle of 45 degrees with regard to body axis, for first whorl. Following half-whorl shows also riblets at an angle of 115 degrees, making the surface pit-reticulated. Whorls 6.5, slightly convex; ultimate whorl about 0.66 total height. Suture deepened. Aperture 0.42 shell height, 1.6 times as long as wide; subovate, whitish inside; apertural deviation five degrees. Peristome thin; columellar margin slightly reflexed and dilated above.

Dimensions of holotype: shell height 19.0, diameter 8.9, height of aperture 8.4, width of aperture 4.5, height of last whorl 13.0; 6.5 whorls.

Type Material: **Holotype:** RMNH 5003990, A. Hovestadt leg., 17 November 2014, from type locality; **Paratypes:** three shells, St. John Windward Parish, above Prison Farm.

Type Locality: Nevis, St. George, Gingerland Parish, along Source trail, North Golden Rock Inn.

Distribution: Endemic to Nevis.



Figures 56–62. Living snails of the family Bulimulidae. 56–60. *Drymaeus (Antidrymaeus) multifasciatus christopherei* Pilsbry, 1899; 61–62. *Drymaeus (Antidrymaeus) multifasciatus* subspecies.

Habitat: Living specimens have been observed crawling on the ground among fallen leaves and climbing on tree trunks, in the wet rainforest.

Remarks: *Bulimulus ouallensis* may be compared to the neighboring species from Saint Kitts, *Bulimulus gittenbergeri* Breure, 1974, from which the new taxon differs by (1) having the sides slightly convex; (2) the light brown color. This new species may also be compared to *Bulimulus lehmanni* (L. Pfeiffer, 1865), occurring on Dog Island, Anguilla and Saint Martin-Sint Maarten, but the latter species has definitely coarser growth striae, lacks the pit-reticulated surface of the protoconch and lacks the sutural tufts; the shell is also more solid. The key to Caribbean *Bulimulus* species (Breure, 1974: 11–12) may be adapted as follows:

- 13a. Sides straight 14
- 13b. Sides slightly convex *B. ouallensis*
- 14a. Colour yellowish to greyish white; aperture white inside *B. gittenbergeri*
- 14b. Colour pale russetbrown; inside aperture coloured like outside *B. fuscus*

Etymology: The specific epithet derives from *Oualla*, the pre-Colombian name for the island, meaning “land

of the beautiful waters”, which presumably refers to the many water sources and the hot volcanic springs on the island.

Genus *Drymaeus* Albers, 1850

Subgenus *Antidrymaeus* L. Germain, 1907

Remarks: In a forthcoming paper, Breure and Robinson will show that several *Drymaeus* species from the Caribbean Basin form a monophyletic group, for which the name *Antidrymaeus* L. Germain, 1907 may be used. The common characteristic in the external morphology of this group is the bluish color of the body, most noticeable in juvenile specimens.

Drymaeus (Antidrymaeus) multifasciatus christopherei Pilsbry, 1899 new combination
(Figures 54, 56–60)

Bulimus multifasciatus Lam[arck], 1822.—Bland, 1862: 358. St. Kitts.

Bulimulus multifasciatus Lamarck, 1822.—Rush, 1891: 69. St. Kitts.

Drymaeus multifasciatus var. *christopherei* Pilsbry, 1899.—16, pl. 13 figs 98–99. St. Christopher.

Drymaeus multifasciatus christopheri Pilsbry, 1899.—Clench and Turner, 1962: 31.

Drymaeus multifasciatus christopheri Pilsbry, 1899.—H.B. Baker, 1963: 227 (lectotype designation).

Survey Material: SAINT KITTS: Christchurch, Nichola Town Parish, trail to Phillips Level (USDA); St. Paul, Capisterre Parish, crater trail up Mount Liamuiga (USDA); Trinity, Palmetto Point Parish, trail to Ottley's Level (AH).

Additional Material Examined: SAINT KITTS: ex Swift coll. (ANSP 25857, lectotype), (ANSP 325063, paralectotypes); T. Bland, ex A.D. Brown (ANSP 3417); (UF 176958).

Distribution: Endemic to Saint Kitts.

Habitat: Occurs in rainforest.

Drymaeus (Antidrymaeus) multifasciatus subspecies (Figures 54, 61–62)

Survey Material: NEVIS: St. George, Gingerland Parish, Herbert Heights, trail up Nevis peak past Rawlin's Entrance, D.G. Robinson leg., 17 March 2004 (USDA); *ibid.*, near Peak Heaven (AH*); St. James, Windward Parish, above Prison Farm, D.G. Robinson leg, 12 March 2004 (USDA); *ibid.* (AH*).

Distribution: Endemic to Nevis.

Habitat: Occurring in cloud forest and rain forest.

Remarks: This subspecies differs from the previous subspecies by the far less brightly-colored adult shell, instead showing dull bands of reddish-brown and yellow, which have a tendency to fade away into the background color; the patch around the umbilicus is also less colored than the material from Saint Kitts.

Family Amphibulimidae P. Fischer, 1873

Genus *Amphibulima* Lamarck, 1805

Amphibulima patula christopheri Pilsbry, 1902 (Figures 42–43)

Succinea patula Brug[uière], 1789.—Bland, 1862: 358. St. Kitts.

Amphibulima patula Bruguière, 1789.—Rush, 1891: 69. *Amphibulima patula* Bruguière, 1789.—Pilsbry, 1899: 234, pl. 61 figs 14–19. St. Kitts, Bayford Estate.

Amphibulima patula var. *christopheri* Pilsbry, 1902.—lxviii, pl. 60 figs 11–12; pl. 62, figs 27–30. St. Kitts.

Amphibulima patula christopheri Pilsbry, 1902.—Clench and Turner, 1962: 31.

Amphibulima patula christopheri Pilsbry, 1902.—H.B. Baker, 1963: 227 (lectotype designation).

Amphibulima patula christopheri Pilsbry, 1902.—Breure, 1973: 53.

Survey Material: SAINT KITTS: St. John Capisterre Parish, crater trail up Mount Liamuiga (USDA); St. Thomas

Middle Island Parish, trail to D'O's Dane Pond, off Old Military trail (USDA); Trinity Palmetto Point Parish, top of Ottley's Level (USDA); NEVIS: St. James Windward Parish, above Prison Farm (USDA).

Distribution: Saint Kitts, Nevis.

Habitat: This semi-slug seems to be restricted to rain and cloud forests.

Remarks: This is the first report for this taxon from Nevis. Another subspecies, from Dominica, has been reported to frequent banana and *Citrus* trees (Robinson et al., 2009: 638).

Superfamily Pupilloidea Turton, 1831

Family Gastrocoptidae Pilsbry, 1918

Genus *Gastrocopta* Wollaston, 1878

Gastrocopta barbadensis (L. Pfeiffer, 1854)

Gastrocopta (Gastrocopta) barbadensis barbadensis (L. Pfeiffer [., 1854]).—Haas 1960: 6, pl. 2 figs A–F. St. Christopher, Brimstone Hill. Nevis, Jessops Village; Jones' River.

Survey Material: Not collected during these surveys.

Additional Material Examined: SAINT KITTS: Brimstone Hill (RMNH). NEVIS: Jessops Village (RMNH); Jones' River (RMNH).

Distribution: West Indies.

Gastrocopta rupicola marginalba (L. Pfeiffer, 1840) (Figures 11, 40)

Gastrocopta (Gastrocopta) rupicola marginalba (L. Pfeiffer[., 1840]).—Haas 1960: 12, pl. 2, fig. K; pl. 5 figs A–D. St. Christopher, Timothy Hill; Frigate Bay; Brimstone Hill.

Survey Material: SAINT KITTS: St. Thomas, Middle Island Parish, base of Brimstone Hill (USDA).

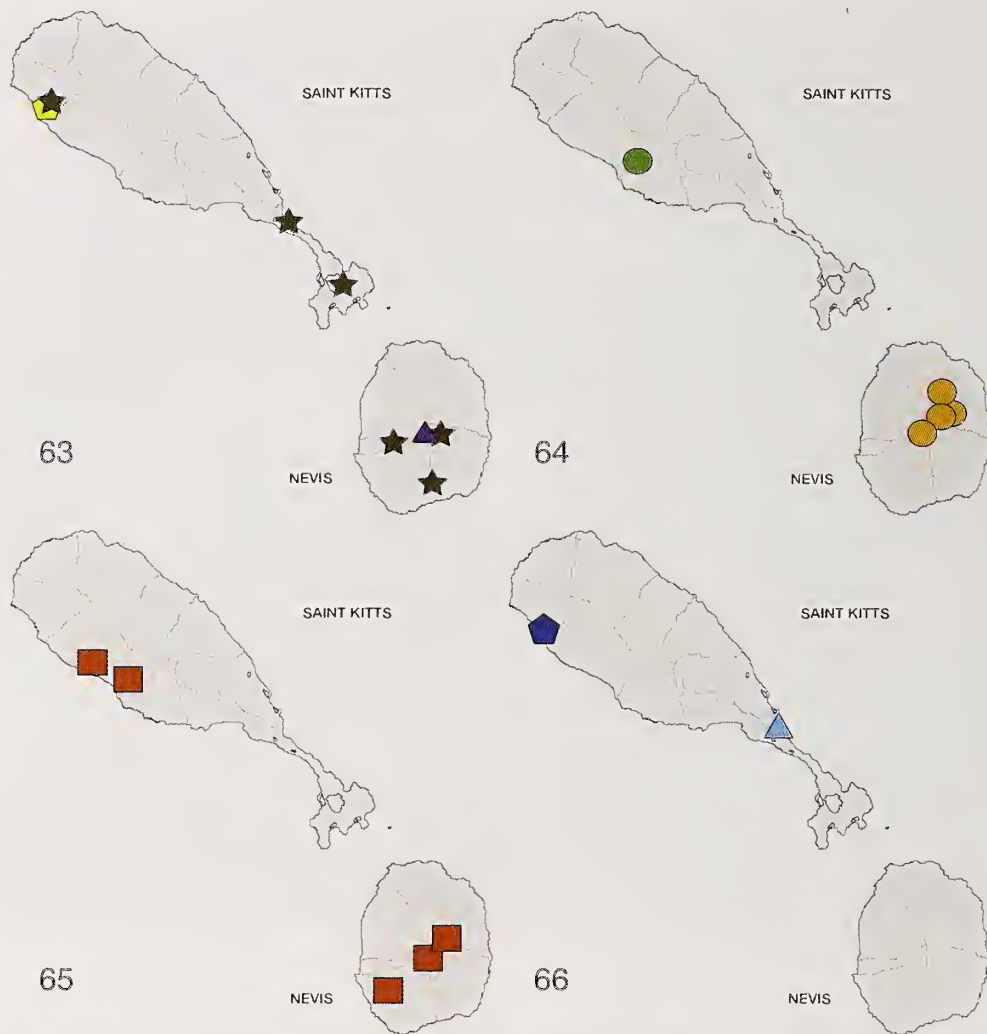
Distribution. Saint Thomas, Saint Croix, Dog Island, Saint Martin, Saint Kitts, southern United States and northern Mexico.

Gastrocopta servilis (Gould, 1843) (Figures 12, 41)

Gastrocopta (Gastrocopta) servilis servilis (Gould [., 1843]).—Haas, 1960: 11, pl. 4 figs F–H. St. Christopher, Morne Hills.

Survey Material: SAINT KITTS: St. George Basseterre Parish, road to Turtle Beach, south of Salt Pan (USDA); St. Thomas Middle Island Parish, base of Brimstone Hill (USDA).

Distribution: West Indies, Central America, Venezuela.



Figures 63–66. Distribution Pupillidae, Sagdidae, Philomycidae, Gastrodontidae, Polygyridae and Pleurodontidae species. 63. *Pupoides marginatus nitidulus* (L. Pfeiffer, 1839) (yellow polygon), *Hojeda* sp. (brown star), *Pallifera* sp. (purple triangle). 64. *Pleurodonte guadeloupensis* ssp. (green circle), *P. josephinae nevisensis* (Pilsbry, 1889) (orange circle). 65. *Zachrysia provisoria* (L. Pfeiffer, 1858) (red rectangle). 66. *Polygyra p. plana* (Dunker in Philippi, 1843) (light blue triangle), *Zonitoides arboreus* (Say, 1817) (dark blue polygon).

Family Pupillidae Turton, 1831

Genus *Pupoides* L. Pfeiffer, 1854

Pupoides marginatus nitidulus (L. Pfeiffer, 1839)
(Figures 13, 63)

Pupoides (*Pupoides*) *marginatus nitidulus* (L. Pfeiffer [1839]).—Haas, 1960: 5, pl. 1 Figure D. St. Christopher, Brimstone Hill; Nevis, Mosquito Bay.

Survey Material: SAINT KITTS: St. Thomas, Middle Island Parish, base of Brimstone Hill (USDA).

Distribution: West Indies.

Superfamily Sagdoidea Pilsbry, 1895

Family Sagdidae Pilsbry, 1895

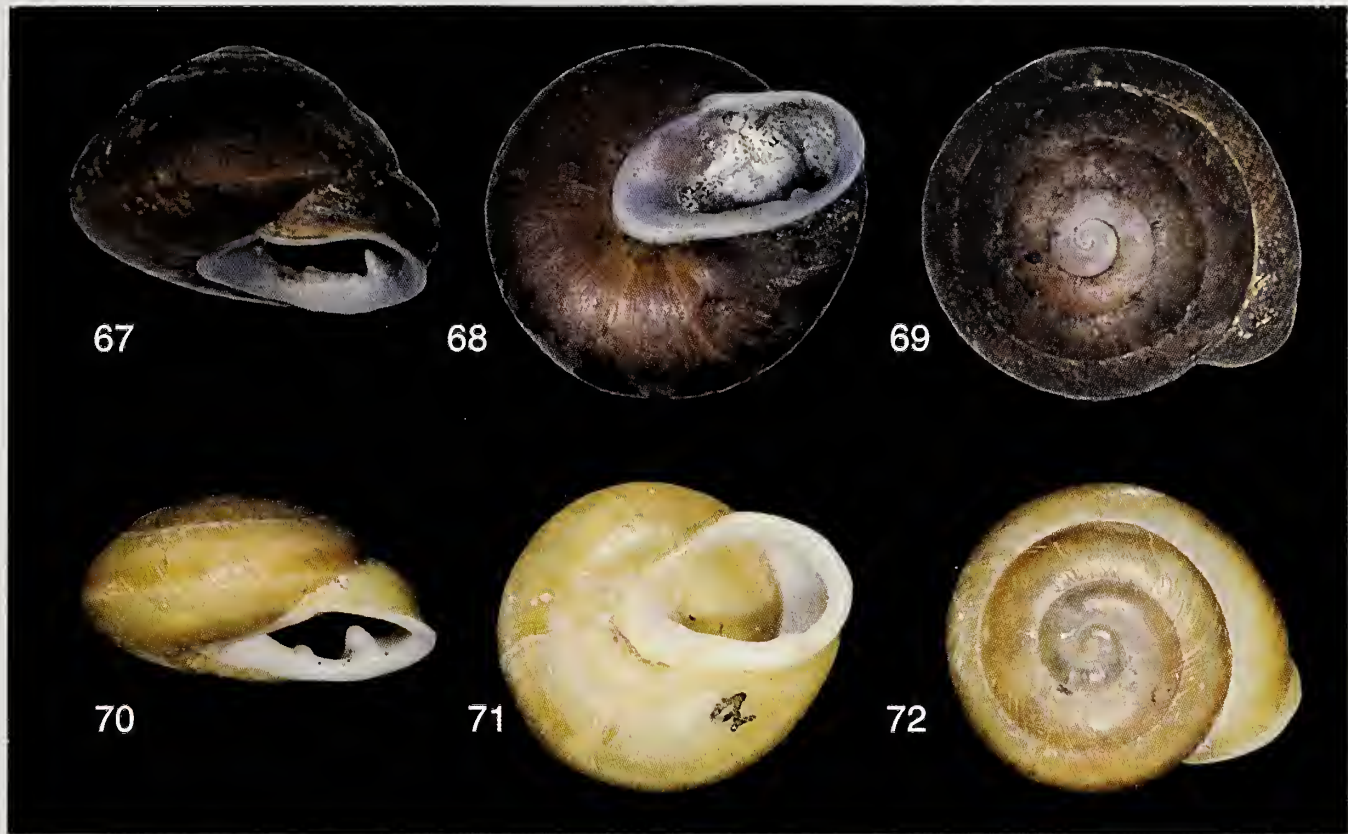
Genus *Hojeda* H.B. Baker, 1926

Hojeda species
(Figures 37–39)

Survey Material: SAINT KITTS: St. George, Basseterre Parish, road to Turtle Beach, south of Salt Pan (USDA); *ibid.*, road south of Basseterre (USDA); St. Thomas, Middle Island Parish, lower slope of Brimstone Hill (USDA); Nevis: St. George, Gingerland Parish, Montravers Estate (AH); St. John, Figtree Parish, Saddle Hill (AH); St. Paul, Charlestown Parish, Hamilton Estate ruins (AH).

Distribution: Guadeloupe, Saint Kitts, Nevis, Saint Eustatius.

Habitat: Found in xerophytic environments on Saint Kitts.



Figures 67–72. Pleurodontidae species. **67–69.** *Pleurodonte guadeloupensis* subspecies, D 14.1 mm. **70–72.** *Pleurodonte josephinae nevisensis* (Pilsbry, 1889), lectotype ANSP 32590, D 17.7 mm.

Remarks: This small sagid (up to 4.5 mm in diameter) closely resembles the Cuban *Hojeda boothiana* (L. Pfeiffer, 1839), but differs by its lower spire, which gives a flatter appearance to the shell. *Hojeda vannattai* H.B. Baker, 1924 from Aruba, and Margarita Island (off the Venezuelan coast) is also very similar but has consistently a somewhat larger umbilicus. Specimens from Saint Eustatius, collected during the late 18th century (ANSP 28312), are virtually identical; similar shells have also been found on Guadeloupe (Robinson, unpublished data).

Superfamily Helicoidea Rafinesque, 1815

Family Polygyridae Pilsbry, 1895

Genus *Polygyra* Say, 1818

Polygyra plana plana (Dunker in Philippi, 1843)
(Figure 66)

Survey Material: SAINT KITTS: Gardens of the Sugar Bay Club, near North Frigate Bay (AH).

Distribution: Bermuda, Saint Kitts.

Habitat: This is an introduced species, occurring in well-watered gardens.

Remarks: This is the first record for this taxon from Saint Kitts and Nevis. The nominal subspecies occurs on Bermuda. Another subspecies, *Polygyra plana bahamensis* Vanatta, 1919, can be found in the Bahamas and the Turks and Caicos Islands.

Superfamily Arionoidea Gray, 1840

Family Philomycidae Gray, 1847

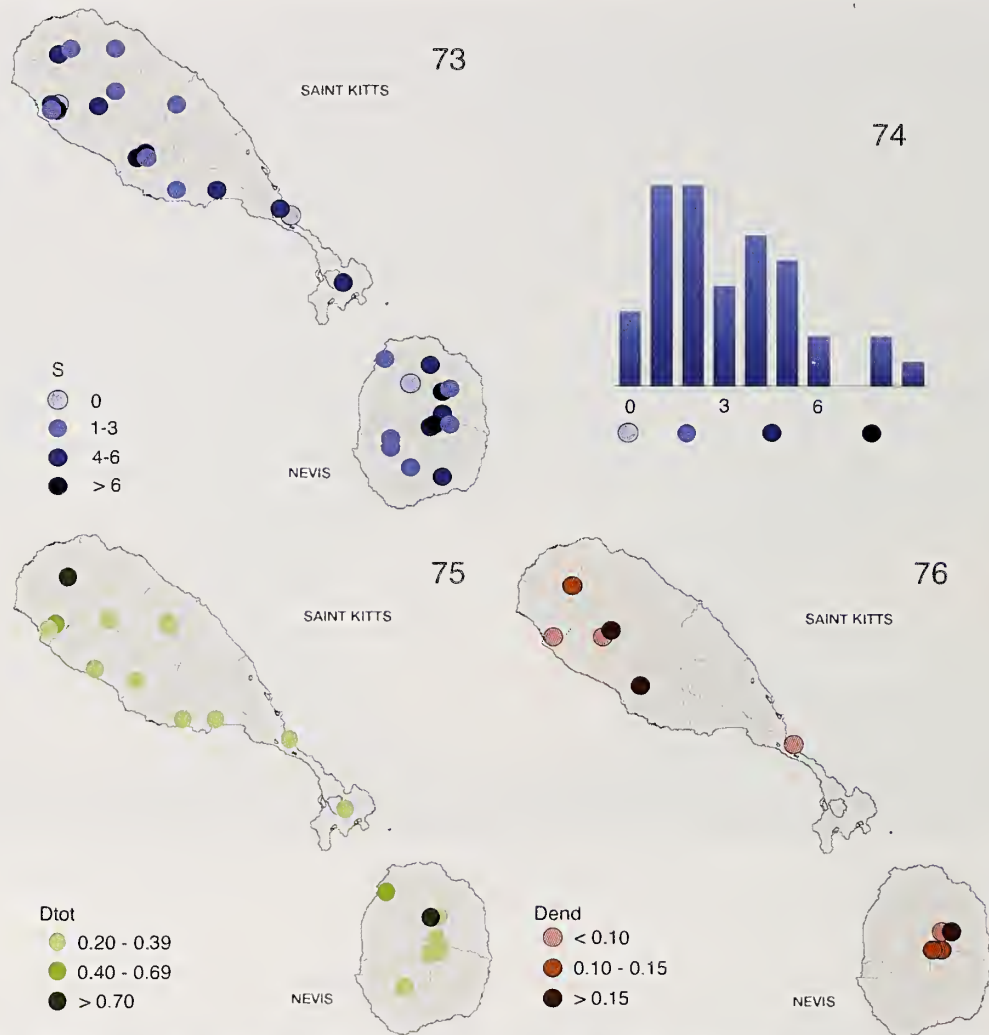
Genus *Pallifera* Morse, 1864

Pallifera species
(Figure 24)

Survey Material: NEVIS: St. George, Gingerland Parish, Herbert Heights, trail to Nevis Peak (USDA).

Distribution: Nevis; USA.

Remarks: This species has been reported from Montserrat (Shoobs and Coote, 2014, as *Pallifera dorsalis* (Binney, 1842)) and Martinique and Guadeloupe (Delannoye et al., 2015, as *P. spec.*). This is the first record for Saint Kitts and Nevis. It is most likely introduced from elsewhere; until its identity can be ascertained, it is not possible to determine its origin at present.



Figures 73–76. Diversity of land snails on Saint Kitts and Nevis. **73.** Species richness per locality. **74.** Frequency of species richness. **75.** Total diversity; calculated using rareness (see methods), only localities scoring 0.20 or higher shown. **76.** Diversity of endemic species (see methods).

Superfamily Helicoidea Rafinesque, 1815

Family Pleurodontidae von Ihering, 1912

Genus *Pleurodonte* Fischer von Waldheim, 1807

***Pleurodonte guadeloupensis* subspecies**
(Figures 64, 67–69)

Survey Material: SAINT KITTS: Trinity Palmetto Point Parish, top of Ottley's Level (USDA); *ibid.*, trail to Ottley's Level (AH).

Distribution: Saint Kitts.

Remarks: This snail belongs to the *Pleurodonte guadeloupensis* species complex of Guadeloupe, Dominica, Saint Martin, and Martinique. It differs from the other subspecies in this complex in being higher-spined, with slightly different labial dentition.

***Pleurodonte josephinae nevisensis* (Pilsbry, 1889)**
(Figures 30, 64, 70–72)

Helix josephinae Fér[ussac], 1832.—Bland 1862: 358; St. Christopher.

Helix (Dentellaria) josephinae Férussac, 1832.—Pilsbry 1889: 88, pl. 29 figs 31–33; Various islands, including subfossils from St. Kitts and Nevis.

Helix josephinae var. *nevisensis* Pilsbry 1889.—89, pl. 25 figs 54–55; Nevis.

Helix (Dentellaria) josephinae nevisensis Pilsbry, 1899.—Clench and Tuner 1962: 104 ["no locality given"; sic].

Helix josephinae nevisensis Pilsbry, 1899.—H.B. Baker, 1963: 246.

Survey Material: NEVIS: St. George, Gingerland Parish, Herbert Heights, trail to Nevis Peak (USDA); *ibid.*, near Peak Heaven (AH); *ibid.*, along Source trail, N Golden Rock Inn (AH); St. James, Windward Parish, above Prison Farm (AH, USDA).

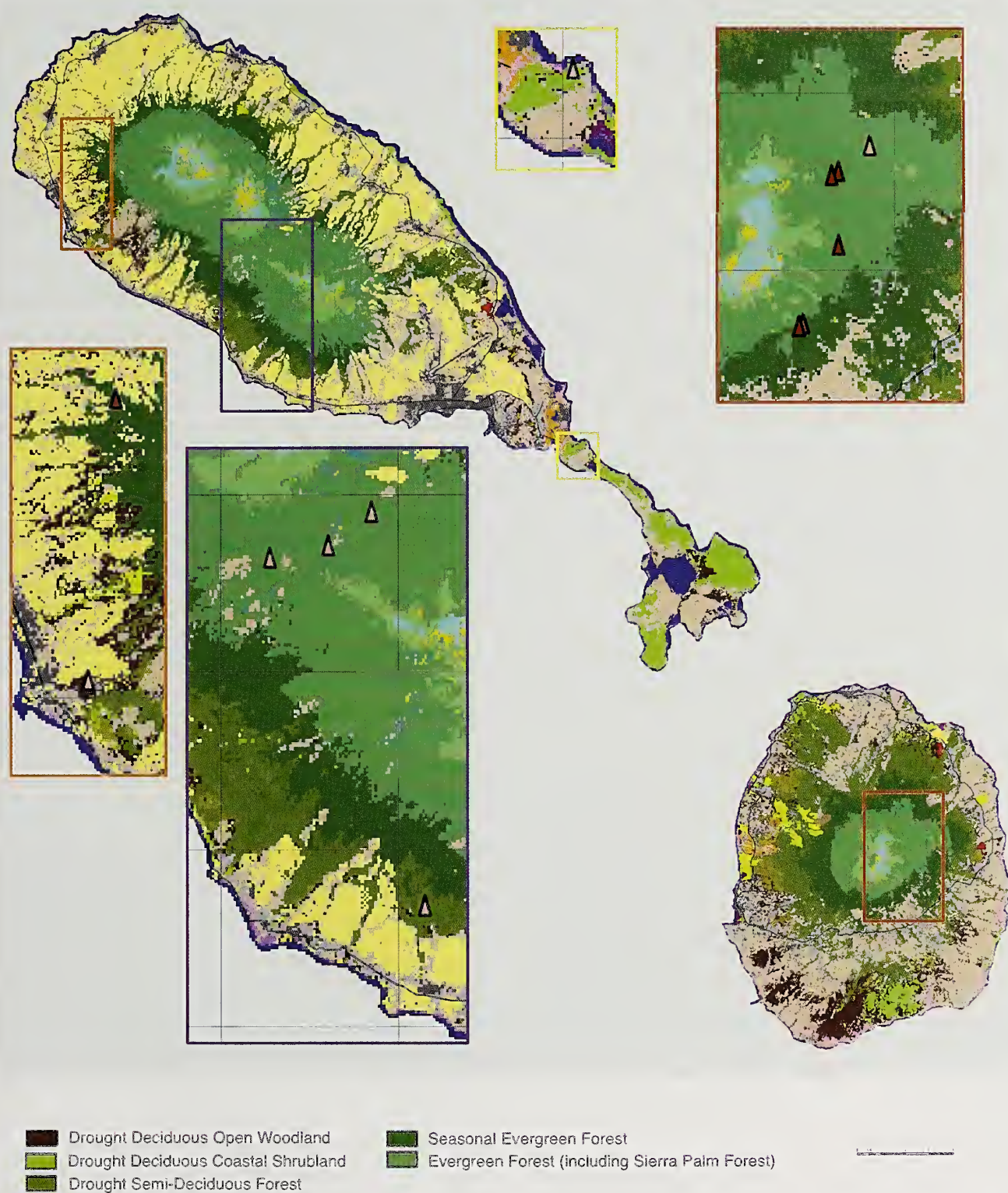


Figure 77. Land cover and forest formations on Saint Kitts and Nevis, 1999–2003, with distribution of endemic species. Modified after Helmer et al. 2006; grid lines refer to the UTM system. Triangles refer to the localities where endemic species were found (light color, one species; dark colored, two species). Enlarged parts of the islands indicated with corresponding colors. Scale = 4 km.

Additional Material Examined: SAINT KITTS: T. Bland leg., ex A.D. Brown (ANSP 1052, subfossil); ex Swift coll. (ANSP 32591, subfossil); J.S. Phillips leg. (ANSP 30907; see remarks); NEVIS: T. Bland leg. (ANSP 32590, syntype); A.D. Brown leg. (ANSP 110428).

Distribution: Saint Kitts?, Nevis.

Habitat: This species exhibits a marked preference for humid conditions in dense vegetation, being particularly abundant on the upper slopes of Nevis Peak.

Remarks: The more widespread *Pleurodonte josephinae* (Férussac), occurring on Guadeloupe, and Dominica, has been reported to occur on both Saint Kitts and Nevis, based on subfossil specimens. However, Pilsbry (1889) recognized the population still living on Nevis as a distinct subspecies; he may have been unaware that the subfossils also belong to this taxon. Two specimens (ANSP 30907) were collected early 20th century on Saint Kitts. One, a fully developed adult, appears to have a higher spire than any of the Nevisian material we have seen. These shells may represent a surviving Kittitian population that we were unable to locate.

Genus *Zachrysia* Pilsbry, 1894

Zachrysia provisoria (L. Pfeiffer, 1858)
(Figure 65)

Survey Material: SAINT KITTS: St. Thomas, Middleland Parish, near Romney Manor (AH); Trinity Palmetto Point Parish, Ottley's Plantation House (AH); NEVIS: St. George, Gingerland Parish, near Peak Heaven (AH); *ibid.*, Montravers Estate (AH*); St. John, Figtree Parish, Prospect, Experimental Station (USDA).

Distribution: Cuba; introduced to Florida, the Bahamas Islands, Cayman Islands, Jamaica, Saint Thomas, Saint Croix, Antigua, Anguilla, Saint Martin-Sint Maarten, Saint Barts, Nevis, Guadeloupe, Barbados, Mustique, Curaçao.

Remarks: This potentially serious horticultural pest appeared to be restricted to a single greenhouse in Nevis at the time of collection (2004). However, during the past decade the species has spread and has now been found at disturbed environments on both islands. It was recently reported as introduced on Guadeloupe (Massemin and Pointier, 2010).

SPECIES DOUBTFULLY OR ERRONEOUSLY REPORTED FROM THE ISLANDS

Due to inaccuracies in provenance of snail specimens (or the total lack of locality data) collected during the 18th and early 19th century, or misidentifications by later authors, the following species have been reported from Saint Kitts. As there is no supporting evidence that these species are actually occurring on one or both islands, these taxa should be removed from the list of terrestrial mollusks from Saint Kitts and Nevis.

Helicina (Analcadia) antillarum G.B. Sowerby II, 1842

Helicina antillarum G.B. Sowerby II, 1842.—Rush, 1891: 67; St. Kitts.

Remarks: This species is distributed on Guadeloupe (but see, Dominica, and Martinique. The record by Rush is likely based on a misidentification. Delannoye et al., 2015, however, indicated that the species is most likely endemic to Martinique). It should be noted that Rush (1891) also reported an unidentified *Helicina* species. We did not encounter any helieinid other than the two reported herein.

Glyphyalina barbadensis Chase and Robinson, 2001

Hyalina incisa L. Pfeiffer, 1866.—Rush 1891: 68; St. Kitts.

Remarks: This taxon was described from Barbados as *Hyalina incisa* by Pfeiffer (1866), and subsequently renamed *Glyphyalina barbadensis* by Chase and Robinson (2001), the original name being unavailable. We did not encounter this zonitoid species during the surveys. It may be that Rush misidentified either immature specimens of *Streptaxis glaber* (Pfeiffer) or the *Hojeda* species mentioned above, whose shells are superficially similar.

Drymaeus (Mesembrinus) virgulatus (Férussac, 1821)

Drymaeus (Mesembrinus) liliaceus Férussac, 1832.—Pilsbry 1889: 11; St. Kitts?

Remarks: Pilsbry reported this taxon from Saint Kitts without giving a reference. We have been unable to trace any specimens collected from the island.

DISCUSSION

Our list of land Mollusca from Saint Kitts and Nevis (Table 3) contains at present 33 taxa, of which six (18%) are confined to one island (single island endemics; SIEs); one taxon is endemic to both islands. Two species have been found which are likely introduced, but at present their systematic position cannot be ascertained. Of the list, 22 species are widespread in the West Indies or beyond (66%). During geological times the areas of these islands have been dynamic and at the height of the Late Glacial Maximum (26,500 to 19,000 years before present) sea levels were ca. 150 m lower (Clark et al., 2009). During this time, Saint Kitts and Nevis were united with Saint Eustatius on the "paleo-island" Saint Kitts-Nevis Bank. This paleo-island, like others in the Lesser Antilles at that time, may have well served as separate biogeographic areas (Peck, 2011). When we take the land snails of Saint Eustatius into account (Hovestadt, 1980), eight taxa (24%) are endemic to this paleo-island; 11 taxa (33%) may be called Lesser Antillean endemics.

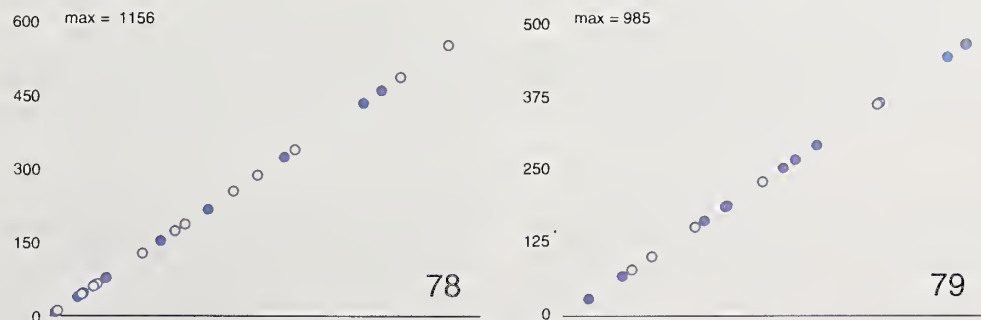
We have furthermore analyzed the fauna with respect to altitudinal occurrence, and whether they occur on the

Table 3. Summary of species, alphabetically arranged, and their distribution. Abbreviations: E, endemic; I, introduced; ×, collected during surveys mentioned in this paper (Saint Kitts and Nevis) or known from literature (other islands);?, questionable reports. Species reported for Saints Kitts and Nevis for the first time are shown in bold type.

Taxon	St. Kitts	Nevis	St. Eustatius	Lesser Antilles, other	Other
<i>Allopeas gracile</i>	X	X	X	X	X
<i>Allopeas micra</i>	X	X	X	X	X
<i>Amphibulima patula christopheri</i>	X	X			
<i>Beckianum beckianum</i>	X	X	X	X	X
<i>Bulimulus diaphanus fraterculus</i>		X	X	X	
<i>Bulimulus gittenbergeri</i>	E				
<i>Bulimulus guadalupensis</i>	X	X	X	X	X
<i>Bulimulus ouallensis</i>		E			
<i>Diplosolenodes</i> sp.		X / I?			
<i>Drymaeus multifasciatus christopheri</i>	E				
<i>Drymaeus multifasciatus subspecies</i>		E			
<i>Gastrocopta barbadensis</i>	X		X	X	X
<i>Gastrocopta rupicola marginata</i>	X	X		X	X
<i>Gastrocopta servilis</i>	X		X	X	X
<i>Helicina fasciata</i>	X	X	X	X	
<i>Hojeda</i> sp.	X	X	X	X	
<i>Huttonella bicolor</i>	I			I	X
<i>Leptinaria unilamellata</i>	X	X		X	X
<i>Lucidella plicatula christophori</i>	X	X			
<i>Obeliscus swiftianus</i>	X			X	X
<i>Pallifera</i> sp.		X / I?			I
<i>Pleurodonte guadeloupensis</i> ssp.	E				
<i>Pleurodonte josephinae nevisensis</i>		E			
<i>Polygyra plana plana</i>	X				X
<i>Pupoides marginatus nitidulus</i>	X		X	X	X
<i>Streptartemon glaber</i>	X	X		X	X
<i>Subulina octona</i>	X	X	X	X	X
<i>Succinea</i> sp. A	X				
<i>Succinea</i> sp. B		X			
<i>Veronicella</i> aff. <i>floridana</i>	X	X		X	X
<i>Veronicella cubensis</i>	X	X		X	X
<i>Zachrysia provisoria</i>	I	I		I	X
<i>Zonitoides arboreus</i>	I		X	X/I?	X

windward (northeast) or leeward (southwest) side of the islands. Although the highest elevations have not been well-sampled (Figures 78–79), some observations may be made. A number of species occur only at lower altitudes, viz. *Succinea* species, *Obeliscus swiftianus*, *Zonitoides arboreus*, *Huttonella bicolor*, *Bulimulus gittenbergeri*, *Gastrocopta* species, *Pupoides marginatus nitidulus*,

Polygyra plana plana, and *Zachrysia provisoria*. With the exception of *Bulimulus gittenbergeri*, these species are largely introduced species. In contrast, a few species seem to be restricted to higher elevations, i.e. above 250 m: *Diplosolenodes* species, *Drymaeus* species, *Amphibulima patula christopheri*, and *Pleurodonte josephinae nevisensis* (Figures 80–81).



Figures 78–79. Altitudinal range of localities sampled. 78. Saint Kitts. 79. Nevis. Dark circles indicate localities at windward side of the island.

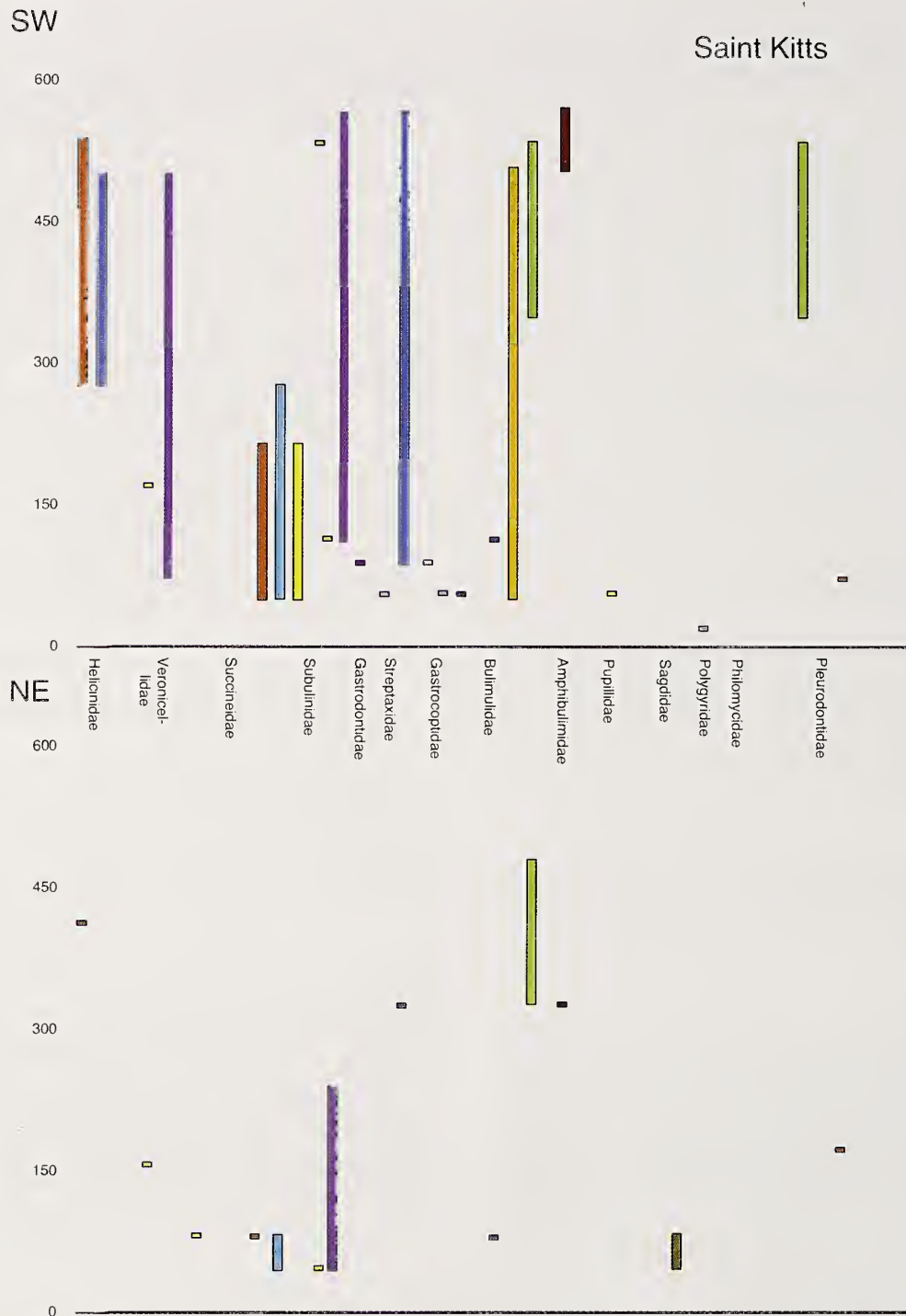


Figure 80. Altitudinal range of species on Saint Kitts, respectively on leeward (upper) and windward (lower) sides of the island. Colours correspond to those used in distribution maps.

When analyzing the localities related to their diversity (see Methods), it is clear that most of them have a rather low species diversity. At four localities no snails were found; at the remaining localities species diversity ranged from 1 to 9 (mean 3.12; Figure 73). Taking the rareness of species into account, the higher elevational localities tend to score higher (Figures 75–76). There are

six species endemic to both islands (of which five are SIEs): *Bulinulus gittenbergeri*, *B. ouallensis*, *Drymaeus* (*Antidrymaeus*) *multifasciatus christopherei*, *D. (A.) m.* subspecies (Nevis), *Amphibulima patula christopherei*, and *Pleurodonte josephinae nevisensis*. The localities where these endemics have been found are given in Figure 77. The data (adapted from Helmer et al., 2006)

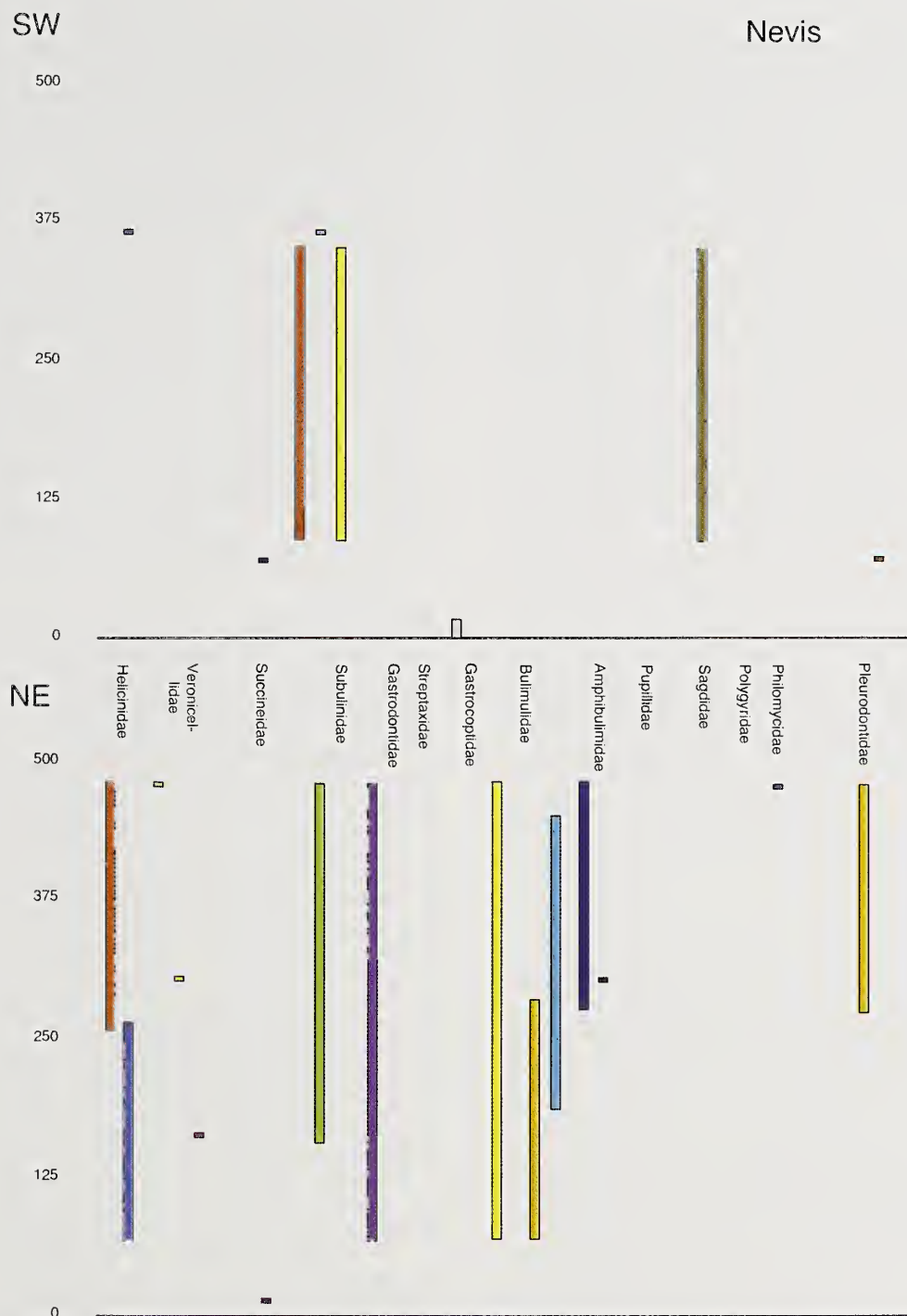


Figure 81. Altitudinal range of species on Nevis, respectively on leeward (upper) and windward (lower) sides of the island. Colours correspond to those used in distribution maps.

show that these endemics occur in five vegetation types, of which three are drought and two are wet types: Drought Deciduous Open Woodland (*Bulimulus gittenbergeri*), Drought Deciduous Coastal Shrubland (*B. gittenbergeri*), Drought Semi-Deciduous Forest (*Drymaeus (Antidrymaeus) multifasciatus christopheri*), Seasonal Evergreen Forest (*D. (A.) multifasciatus christopheri*, *D. (A.) m. subspecies*

(Nevis), *Amphibulima patula christopheri*, *Pleurodonte josephinae nevisensis*), and Evergreen Forest (*B. ouallensis*, *D. (A.) m. subspecies* (Nevis), *P. josephinae nevisensis*). Although similar detailed data were not available to us when writing our study on Dominica (Robinson et al., 2009), we notice a similar pattern: endemic species are predominantly found in the wet vegetation types at higher elevations.

In this context it is interesting to take the protection status of the land snail habitats into account. Helmer et al. (2008) concluded that during 1949–2000 the land cover on both islands has changed dramatically, but a common aspect is that agricultural land (sugar cane plantations) has changed into pasture land. Dry and humid forests increased in area (respectively with 50% for Saint Kitts and 134% for Nevis respectively) during this period. Proportional increases in drier formations at lower elevations were larger than those in evergreen formations at higher elevations. The degree of (formal) protection, however, varies for different categories, ranging from 100% for Evergreen Forest to 0% for lowland Drought (Semi-)Deciduous Forest (Helmer et al., 2008, table 5). Gardner (2006) showed that institutional frameworks for area protection and protected area programs are hardly developed on the islands. As pressure for land development is greatest at lower elevations (Helmer, 2004), lowland drought shrubland and forest are not well protected. Hence snail species occurring there may be vulnerable to habitat fragmentation or destruction. Lugo et al. (2011) suggested that, due to land cover changes in built-up and degraded lands, introduced taxa may have a competitive edge at lowland elevations. From the data presented on the lowland species, *Bulimulus gittenbergeri* especially may be considered as vulnerable when judged against the IUCN-criteria of Critically Endangered species (IUCN, 2012).

In a recent study, Horwith and Kindsay (1999) stated that data on invertebrates were very limited and information useful to conservation planning was lacking. This void is filled herein for the land snail fauna of these two islands.

ACKNOWLEDGMENTS

We would like to gratefully acknowledge the support of the Departments of Agriculture in both Saint Kitts and Nevis during the 2004 survey. In Saint Kitts, we would like to thank Director of Agriculture Dr Jerome Thomas, Mr Kevin Walters, Mr Thomas Jackson, Mr Lawrence Knight, and Mr Husaini Mawnlawde, all of the Department of Agriculture, Ministry of Agriculture. Of the Nevis Island Administration, we would like to thank Junior Minister J. Livingston Herbert, Director of Agriculture Mr Samuel Powell, Mr Floyd Liburd, and Mr Dwight Browne, all the Department of Agriculture, Ministry of Agriculture, Lands, Housing, Co-operatives and Fisheries, for their support of the USDA project. Finally we thank Ton de Winter for help with the photograph of the new species. Laurent Charles and Thomas Watters kindly provided comments on a previous version of this manuscript, which helped to improve it.

LITERATURE CITED

- Albers, J.C. 1850. Die Heliceen, nach natürlicher Verwandtschaft systematisch geordnet. Enslin, Berlin, 262 pp.
- Albers, J.C. 1860. Die Heliceen, nach natürlicher Verwandtschaft systematisch geordnet. 2e Ausgabe (ed. E. von Martens). Engelmann, Leipzig, xviii + 359 pp.
- Anonymous. 1991. Country environmental profile St. Kitts and Nevis. The Caribbean Conservation Association, St. Michael (Barbados), 277 pp.
- Armstrong, P. 1990. The english parson-naturalist. A companionship between science and religion. Gracing, Leominster, x + 198 pp.
- Baker, H.B. 1923. The Mollusea collected by the University of Michigan-Williamson expedition in Venezuela. Occasional Papers of the Museum of Zoology, University of Michigan 137: 1–50.
- Baker, H.B. 1926. Anatomical notes on American Helicinidae. Proceedings of the Academy of Natural Sciences of Philadelphia 80: 1–44.
- Baker, H.B. 1935. Jamaican land snails, 3. The Nautilus 48: 83–88.
- Baker, H.B. 1961. *Beckianum*. The Nautilus 75: 84.
- Baker, H.B. 1963. Type land snails in the Academy of Natural Sciences of Philadelphia Part II. Land Pulmonata, exclusive of North America north of Mexico. Proceedings of the Academy of Natural Sciences of Philadelphia 115: 191–259.
- Beard, J.S. 1949. The natural vegetation of the Windward and Leeward Islands. Oxford University Press, Oxford, 192 pp.
- Beck, H.H. 1837–1838. Index molluscorum praesentis aevi musei principis augustissimi Christiani Frederici. Hafniae, 124 pp.
- Binney, A. 1851. The terrestrial air-breathing mollusks of the United States and adjacent territories of North America, I. Little and Brown, Boston, 366 pp.
- Blainville, M.H.D. de 1817. Mémoire sur quelques mollusques pulmobranches. Journal de Physique de Chimie et d'Histoire Naturelle (Paris) 85: 437–444.
- Bland, T. 1862. On the geographical distribution of the genera and species of land shells of the West Indian island; with a catalogue of the species of each island. Annals of the Lyceum of Natural History of New York 7: 335–361.
- Boss, K.J. and M.K. Jacobson. 1974. Catalogue of the taxa of *Lucidella* (Prosobranchia: Helicinidae). Occasional Papers on Mollusks 4 (49): 29–38.
- Bouchet, P., J. Fryda, B. Hausdorf, W. Ponder, A. Valdés, and A. Warén. 2005. Working classification of the Gastropoda. Malacologia 47: 240–283.
- Breure, A.S.H. 1973. Catalogue of Bulimulidae (Gastropoda, Euthyneura), I. Amphibuliminae. Basteria 37: 51–56.
- Breure, A.S.H. 1974. Caribbean land molluscs: Bulimulidae. I. *Bulimulus*. Studies on the Fauna of Curaçao and other Caribbean Islands 45: 1–80.
- Bruguière, J.G. 1789–1792. Encyclopédie méthodique. Histoire naturelle des vers, I. Pancoucke, Paris, xviii + 757 pp.
- Chase, R. and D.G. Robinson. 2001. The uncertain history of land snails on Barbados: implications for conservation. Malacologia 43: 33–57.
- Clark, P.U., A.S. Dyke, J.D. Shakun, A.E. Carlson, J. Clark, B. Wohlfarth, J.X. Mitrovica, S.W. Hoestetler and A.M. McCabe. 2009. The last glacial maximum. Science 325: 710–714.
- Clench, W.J. 1956. Land shells of Barbuda Island, Lesser Antilles. The Nautilus 70: 69–70.
- Clench, W.J. and R.D. Turner. 1962. New names introduced by H.A. Pilsbry in the Mollusca and Crustacea. Special Publications of the Academy of Natural Sciences of Philadelphia 4: 1–218.
- Delannoye, R., L. Charles, J.-P. Pointier, and D. Massemin. 2015. Mollusques continentaux de la Martinique. Non-marine molluscs of Martinique, Lesser Antilles. Biotope/Muséum nationale d'Histoire naturelle, Mèze/Paris, 326 pp.

- Draparnaud, J.P.R. 1801. Tableau des mollusques terrestres et fluviatiles de France. Renaud, Montpellier, 116 pp.
- Férussac, A.E.J.P.J.F. d'Audebard. 1821–1822. Tableaux systématique des animaux mollusques suivis d'un Prodrôme général pour tous les mollusques terrestres ou fluviatiles vivants ou fossiles. Baillière, Paris, xlvii + 110 pp.
- Fischer, P. 1873. Note sur l'animal du *Succinea rubescens*. Journal de Conchyliologie 21: 324–325.
- Fischer, P. and H. Crosse. 1870–1878. Études sur les mollusques terrestres et fluviatiles du Mexique et du Guatemala. In: Milne Edwards, A. (ed.), Mission scientifique au Mexique et dans l'Amérique Centrale. Recherches zoologiques 7 (1). Imprimerie Nationale, Paris, 702 pp.
- Fischer von Waldheim, G. 1807. Museum Demidoff, ou catalogue systématique et raisonné des curiosités de la nature et de l'art, 3. Moskau, 330 pp.
- Gardner, L. 2006. Review of the policy, legal and institutional frameworks for protected areas management in St. Kitts and Nevis. Environment and Sustainable Development Unit, Organisation of Eastern Caribbean States, Castries (St. Lucia), 87 pp.
- Germain, L. 1907. Sur quelques mollusques de l'Équateur. Bulletin du Muséum national d'Histoire naturelle, Paris 13: 52–64.
- Gould, A. 1843. Monograph of the species of *Pupa* found in the United States. Boston Journal of Natural History 4: 350–360.
- Gray, J.E. 1840. Shells of molluscos animals. Synopsis of the contents of the British Museum (42): 105–152.
- Gray, J.E. 1847. A list of the genera of recent mollusca, their synonyms and types. Proceedings of the Zoological Society of London 15: 129–206.
- Gray, J.E. 1860. On the arrangement of the land pulmoniferous Mollusca into families. Annals and Magazine of Natural History (3) 6: 267–269.
- Haas, F. 1960. Caribbean land molluscs: Vertiginidae. Studies on the Fauna of Curaçao and other Caribbean Islands 10: 1–17.
- Haas, F. 1962. Caribbean land molluscs: Subulinidae and Oleacinidae. Studies on the Fauna of Curaçao and other Caribbean Islands 13: 49–60.
- Helmer, E.H. 2004. Forest conservation and land development in Puerto Rico. Landscape Ecology 19: 29–40.
- Helmer, E.H., T.A. Kennaway, H. Marciano-Vega, M.L. Clark, and T.R. Ruzyski. 2006. Map of land cover and forest formations of St. Kitts, Nevis, and St. Eustatius 1999–2003. International Institute of Tropical Forestry, Rio Piedras. Available at <http://tinyurl.com/jkv8sev> (accessed 27 January 2015).
- Helmer, E.H., T.A. Kennaway, D.H. Pedreros, M.L. Clark, H. Marciano-Vega, L.L. Tieszen, T.R. Ruzyski, S.R. Sehill, and C.M.S. Carrington. 2008. Land cover and forest formation distributions for St. Kitts, Nevis, St. Eustatius, Grenada and Barbados from decision tree classification of cloud-cleared satellite imagery. Caribbean Journal of Science 44: 175–198.
- Horvith, B. and K. Lindsay. 1999. A biodiversity profile of St. Kitts and Nevis. Island Resources Foundation, St. John's (Antigua), 81 pp.
- Hovestadt, A. 1980. De landslakken van St. Eustatius. Correspondentieblad van de Nederlandse Malacologische Vereniging 195: 1042–1044.
- Hutton, C.O. 1968. The mineralogy and petrology of Nevis, Leeward Islands, British West Indies: A progress report. Transactions of the Fourth Caribbean Geological Conference: 383–388.
- Hutton, C.O. and S.R. Nockolds. 1978. The petrology of Nevis, Leeward Islands, West Indies. Institute of Geological Sciences, Overseas Geology and Mineral Resources 52: 1–31.
- Hutton, T. 1834. On the land shells of India. Journal of the Asiatic Society of Bengal 3: 81–93.
- Ihering, H. von 1912. Analyse der Süd-Amerikanischen Heliceen. Journal of the Academy of Natural Sciences of Philadelphia (2) 15: 475–500.
- IUCN 2012. IUCN Red List criteria and categories, 2nd edition. IUCN, Gland, iv + 32 pp.
- Kobelt, W. 1905–1906. Die Raublungschnecken (Agnatha). Abtheilung 2. Streptaxidae und Daudebardiidae. Systematisches Conchylien-Cabinet von Martini und Chemnitz (2) 1 (12B: 2): 1–211.
- Lamarck, J.B.P.A. 1799. Prodrôme d'une nouvelle classification des coquilles. Mémoires de la Société d'Histoire Naturelle de Paris 1: 63–91.
- Lamarck, J.B.P.A. 1805. Sur l'Amphibulime. Annales du Muséum d'Histoire Naturelle, Paris 6: 303–306.
- Lamarck, J.B.P.A. 1822. Histoire naturelle des animaux sans vertèbres, 6 (2). Verdière, Paris, 232 pp.
- Leach, W.E. 1814. The zoological miscellany; being descriptions of new, or interesting animals, 1. Nodder and Son, London, 144 pp.
- Lehmann, [J.C.R.] 1862. Ueber eine neue Heliceen-Gattung. Malazoologische Blätter 9: 111–112.
- Lindsay, K. and B. Horvith. 1999. A vegetation classification of St. Kitts and Nevis: Implications for conservation. Island Resources Foundation, St. John's (Antigua), 68 pp.
- Lugo, A.E., E.H. Helmer and E. Santiago Valentin. 2011. Paisagens do Caribe e sua biodiversidade. Interciencia 37: 706–710.
- Massemin, D. and J.-P. Pointier. 2010. Ces escargots qui envahissent la Guadeloupe. Le Courrier de la Nature 254: 16–17.
- Martin-Kaye, P.H.A. 1959. Reports on the Geology of the Leeward and British Virgin Islands. Voice Publishing Co., Castries (St. Lucia), 117 pp.
- Morse, E.S. 1864. Observations on the terrestrial pulmonifera of Maine, including a catalogue of all the species of terrestrial and fluviatile Mollusca known to inhabit the State. Journal of the Portland Society of Natural History 1: 1–63.
- d'Orbigny, A. 1835–1847. Voyage dans l'Amérique méridionale exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833, 5 (3), Mollusques. Bertrand, Paris and Levrault, Strasbourg, 758 pp.
- Peck, S.B. 2011. The diversity and distributions of the beetles (Insecta: Coleoptera) of the northern Leeward Islands, Lesser Antilles (Anguilla, Antigua, Barbuda, Nevis, Saba, St. Barthélemy, St. Eustatius, St. Kitts, and St. Martin-St. Maarten). Insecta Mundi 678: 1–54.
- Pfeiffer, L. 1839. Bericht über die Ergebnisse meiner Reise nach Cuba im Winter 1838–1839. Archiv für Naturgeschichte 5: 346–358.
- Pfeiffer, L. 1840. Uebersicht der im Januar, Februar und März 1839 auf Cuba gesammelten Mollusken. Archiv für Naturgeschichte 6: 250–261.
- Pfeiffer, L. 1846. Symbolae ad Historiam Heliciorum, 3. Fischeri, Cassel, 100 pp.
- Pfeiffer, L. 1849. Descriptions of twenty-four new species of Helicea, from the collection of H. Cuming, Esq. Proceedings of the Zoological Society of London 17: 126–131.
- Pfeiffer, L. 1854. Zur Molluskenfauna der Insel Cuba. Malakozoologische Blätter 1: 170–213.

- Pfeiffer, L. 1856. Versuch einer Anordnung der Heliceen nach natürlichen Gruppen. *Malakozoologische Blätter* 2: 145–185.
- Pfeiffer, L. 1858. Zur Molluskenfauna der Insel Cuba. *Malakozoologische Blätter* 5: 37–49.
- Philippi, R.A. 1842–1845. Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien, I. Fischer, Cassel, 204 pp.
- Pilsbry, H.A. 1889. *Helicidae*, vol. 111. *Manual of Conchology* (2) 5: 1–216.
- Pilsbry, H.A. 1893–1895. *Helicidae*, Vol. 7. Guide to the study of *Helices*. *Manual of Conchology* (2) 9: i–xlviii + 1–366.
- Pilsbry, H.A. 1895. Index to *helices*. *Manual of Conchology* (2) 9, Appendix: 1–126.
- Pilsbry, H.A. 1897. A new variety of *Helicina plicatula* Pfr. *The Nautilus* 10: 118.
- Pilsbry, H.A. 1897–1898. American *Bulimulidae*: *Bulimulus*, *Neopetraeus*, *Oxychona*, and South American *Drymaeus*. *Manual of Conchology* (2) 11: 1–339.
- Pilsbry, H.A. 1899. American *Bulimulidae*: North American and Antillean *Drymaeus*, *Leiostracus*, *Orthalicinae* and *Amphibuliminae*. *Manual of Conchology* (2) 12: 1–258.
- Pilsbry, H.A. 1902. Classification of *Bulimulidae* and index to volumes 10–14. *Manual of Conchology* (2) 14: i–xcix.
- Pilsbry, H.A. 1916–1918. *Pupillidae* (Gastropodinae). *Manual of Conchology* (2) 16: xii + 380 pp.
- Potiez, V.L.V. and A.L.G. Michaud, 1838–1844 [1835–1844]. *Galerie des mollusques, ou catalogue méthodique, descriptif et raisonné des mollusques et coquilles du Muséum de Douai*, I. Baillière, Paris, xxvi + 560 pp.
- Rafinesque, C.S. 1815. *Analyse de la nature ou tableau de l'univers et des corps organisés*. Palerme, 233 pp.
- Robinson, D.G., A. Hovestadt, A. Fields and A.S.H. Breure. 2009. The land Mollusca of Dominica (Lesser Antilles), with notes on some enigmatic or rare species. *Zoologische Mededelingen Leiden* 83: 615–650.
- Rush, W.H. 1891. List of species collected on the islands St. Thomas, St. Kitts, Barbados, Jamaica and at Pensacola, Florida; with prefatory notes. *The Nautilus* 5: 65–70.
- Say, T. 1818. Account of two new genera, and several new species, of fresh water and land shells. *Journal of the Academy of Natural Sciences of Philadelphia* 1: 276–284.
- Shoobs, N. and T. Coote, 2014. The terrestrial and freshwater gastropods of Montserrat: an unprecedented survey of Montserratian neotropical snails. Poster presented at Mollusca 2014 Conference, Mexico City. Available at doi:10.13140/2.1.2675.7929 (accessed 18 April 2016).
- Shorthouse, D.P. 2010. SimpleMapp, a web-enabled tool to produce publication-quality point maps. Available at <http://www.simplmapp.net> (accessed 20 February 2015).
- Shuttleworth, J.R. 1854. Beiträge zur näheren Kenntniss der Land- und Süßwasser-Mollusken der Insel Portorico. *Mittheilungen Naturforschende Geseellschaft Bern* 1854 (314–316): 33–56.
- Sowerby II, G.B. 1842–1847. *Thesaurus conchyliorum, or monographs of genera of shells*, I. Sowerby, London, 438 pp.
- Swainson, W. 1840. A treatise on malacology or shells and shellfish. Longman, London, viii + 419 pp.
- Thomé, J.W. 1975. Os gêneros da família Veronicellidae nas Américas (Mollusca: Gastropoda). *Iheringia Zoologia* 48: 3–56.
- Thompson, F.G. 1980. Proserpinoid land snails and their relationships within the Archaeogastropoda. *Malacologia* 25: 1–33.
- Toothill, J., C. Williams, R. MacDonald, S.P. Turner, N.W. Rogers, C.J. Hawkesworth, D.A. Jerram, C.J. Ottley, and A.G. Tindle. 2007. A complex petrogenesis for an arc magmatic suite, St. Kitts, Lesser Antilles. *Journal of Petrology* 48: 3–42.
- Trechmann, C.T. 1932. Notes on Brimstone Hill, St. Kitts. *Geological Magazine* 69: 241–264.
- Tryon, G.W. 1866. Monograph of the terrestrial Mollusca of the United States. *American Journal of Conchology* 2: 218–177.
- Tryon, G.W. 1867. Monograph of the terrestrial Mollusca of the United States. *American Journal of Conchology* 3: 155–181.
- Tryon, G.W. 1885. Testacellidae, Oleacinidae, Streptaxidae, Helicoidea, Vitrinidae, Limacidae, Arionidae. *Manual of Conchology* (2) 1: 1–364.
- Turton, W. 1831. A manual of the land and fresh-water shells of the British Islands. Longman, Reese, Orme, Brown and Greene, London, viii + 152 + 16 pp.
- Wagenaar Hummelinck, P. 1953. Description of new localities. *Studies on the Fauna of Curaçao and other Caribbean Islands* 4: 1–89.
- Westerman, J.H. and H. Kiel. 1961. The geology of Saba and St. Eustatius, with notes on the geology of St. Kitts, Nevis and Montserrat (Lesser Antilles). *Uitgaven Natuurwetenschappelijke Studiekring voor Suriname en de Nederlandse Antillen* 24: xiii + 175 pp.

Comparative anatomy of five species of *Saccostrea* Dollfus and Dautzenberg, 1920 (Bivalvia: Ostreidae) from the Pacific Ocean

Vanessa Simão do Amaral

Luiz Ricardo L. Simone

Museu de Zoologia da Universidade de São Paulo

Caixa Postal 42494

04299-970 São Paulo, BRASIL

vanessasimao@usp.br

lrsimone@usp.br

ABSTRACT

Ostreids are well known for their high intraspecific variation, which makes identification problematic. The present paper provides a morpho-anatomical analysis of five species of *Saccostrea*, as well as of selected congeneric species from relevant areas in the Pacific Ocean. *Saccostrea cucullata* occurs in Africa, Indian Ocean, Arabian Sea, Red Sea, and part of the Pacific, where it lives attached to rocks and mangroves roots. *Saccostrea glomerata* occurs in the Pacific, New Zealand, Australia and the Philippines, always associated with rocks. *Saccostrea echinata* occurs from East Africa to Japan. *S. palmula* occurs from Pacific Mexico to Peru. *Saccostrea mordax* occurs in the Red Sea and the Pacific. The wide distribution and plasticity of these often sympatric species led to confusion regarding their identity. Herein we describe anatomical differences that allow for a more precise identification, especially when compared to sympatric taxa.

Additional Keywords: oyster, morphology, systematics, phenotypic plasticity

INTRODUCTION

Species of the genus *Saccostrea* Dollfus and Dautzenberg, 1920 are oysters that live on rocky shores of the Indo-Pacific region. The taxonomy of this genus is unclear, and their morphological plasticity makes identification problematic (Lam and Morton, 2006). They have small to medium-sized shells, and a left valve with a prominent ligament area, with projections in zigzag continuous and regular. The right valve is flat, bearing projections along its margin, with corresponding concavities on the left valve. The genus includes nine species (Huber, 2010): *Saccostrea cucullata* (Born, 1778) – the type species; *Saccostrea cirumsuta* (Gould, 1850); *Saccostrea echinata* (Quoy and Gaimard, 1835); *Saccostrea glomerata* (Gould, 1850); *Saccostrea kegaki* Torigoe and Inaba, 1981; *Saccostrea malabonensis* (Faustino, 1932); *Saccostrea*

palmula (Carpenter, 1857); *Saccostrea scyphophilla* (Peron and Lesueur, 1807) and *Saccostrea spatulata* (Lamarck, 1819).

Because of shell plasticity, the taxonomy of *Saccostrea* has been a troublesome matter; e.g., some “forms” of *S. cucullata* have been assigned different names by different authors, i.e., *S. echinata*, *S. mordax*, *S. glomerata* (Lam and Morton, 2004). Molecular studies (e.g., Lam and Morton, 2004; 2006; 2009; Wang and Guo, 2008a; 2008b) have been conducted in attempts to resolve this taxonomic confusion and better understand the generic distribution. Reports on the difficulty of proper species identification, caused by the wide variation in body size and coloration, are frequent in the literature and determine a baffling scenario (Awati and Rai, 1931). This problem was further confirmed by Lam and Morton (2006: 1): “The geographical distribution of lineages of *Saccostrea* is somewhat uncertain because of taxonomic confusion”. Moreover, the widespread, sometimes overlapping, distributions of these species also make identification problematic (Huber, 2010).

Molecular systematic studies of *Saccostrea* are few and constrained by many taxonomical issues (Lam and Morton, 2006). Furthermore, the genus has been reported to display ecomorphological variation (Tack et al., 1992). For instance, these facts may help explain why all *Saccostrea* species from Thailand were previously assumed to be a single species, *S. cucullata* (Visoothiviseth et al., 1998). However, the results of Klinbunga et al. (2005) indicated that more than one species of *Saccostrea* may be present in Thai waters, which may have implications regarding its commercial use.

In this paper, we perform a detailed morpho-anatomical study of five *Saccostrea* species from the Pacific Ocean: *S. cucullata*, from Africa, the Indian and Arabian Oceans, the Red Sea and part of the Pacific Ocean; *S. glomerata*, from the Pacific, New Zealand, Australia and the Philippines; *S. echinata*, from East

Africa and Japan; *S. palmula* from Mexico to Peru, in the Pacific and *S. mordax*, from the Red Sea and the Pacific Ocean.

MATERIALS AND METHODS

The study material was preserved in 70–99% ethanol. Specimens were immersed in the preservative fluid and dissected by standard techniques under a stereomicroscope (Simone, 1997; 2009; 2011). Details of all systems (mantle cavity, mantle edge, muscles, digestive, circulatory, excretory, and nervous systems) and organs were examined. Drawings were done with the aid of a *camera lucida*.

The studied samples are held at several institutional collections: National Museum of Natural History, Smithsonian Institution (USNM), Florida Museum of Natural History (UF), Field Museum of Natural History (FMNH), and Museu de Zoologia da Universidade de São Paulo (MZSP).

The following abbreviations are used in the figures: accessory heart (**ah**), adductor muscle (**am**), anus (**an**), auricles (**au**), chomata (**ch**), dorsal hood (**dh**), esophagus (**oe**), external fold (**ef**), gastric shield (**gs**), gills (**gi**), heart (**he**), hood (**ho**), inner fold (**if**), intestine (**in**), mantle edge (**me**), middle fold (**mf**), muscle scar (**im**), pallial muscles (**pm**), palps (**pa**), Quenstedt muscle (**qm**), rectum (**rt**), sorting area (**sa**), typhlosole (**ty**), umbonal cavity (**uc**), undulations (**pl**), ventricle (**ve**), visceral ganglia (**vg**), visceral mass (**vm**).

SYSTEMATICS

Genus *Saccostrea* Dollfus and Dautzenberg, 1920

Type Species: *Ostrea sacculus* Dujardin, 1835 (= *O. cucullata* Born, 1778)

Diagnosis: Shell cup-shaped, with marginal denticles, promial chamber on the right side.

Distribution: This genus is restricted to tropical and sub-tropical waters from eastern Atlantic, Indo-West Pacific, and eastern Pacific, while it is absent in the western Atlantic; in saline areas (open ocean), but occasionally occurring in mangrove areas. Most species live exposed, fixed on rocks or coral (Harry, 1985).

***Saccostrea cucullata* (Born, 1778)**
(Figures 1–15)

Ostrea cucullata [sic] Born, 1778: 100.

Ostrea cucullata Born, 1780: 114, pl. 6, figs 11, 12; Dillwyn, 1817: 277; Smith, 1890: 322; Awati and Rai, 1931: 1–107.

Ostrea cornucopiae Gmelin, 1791: 3336; Küster, 1868: 77.

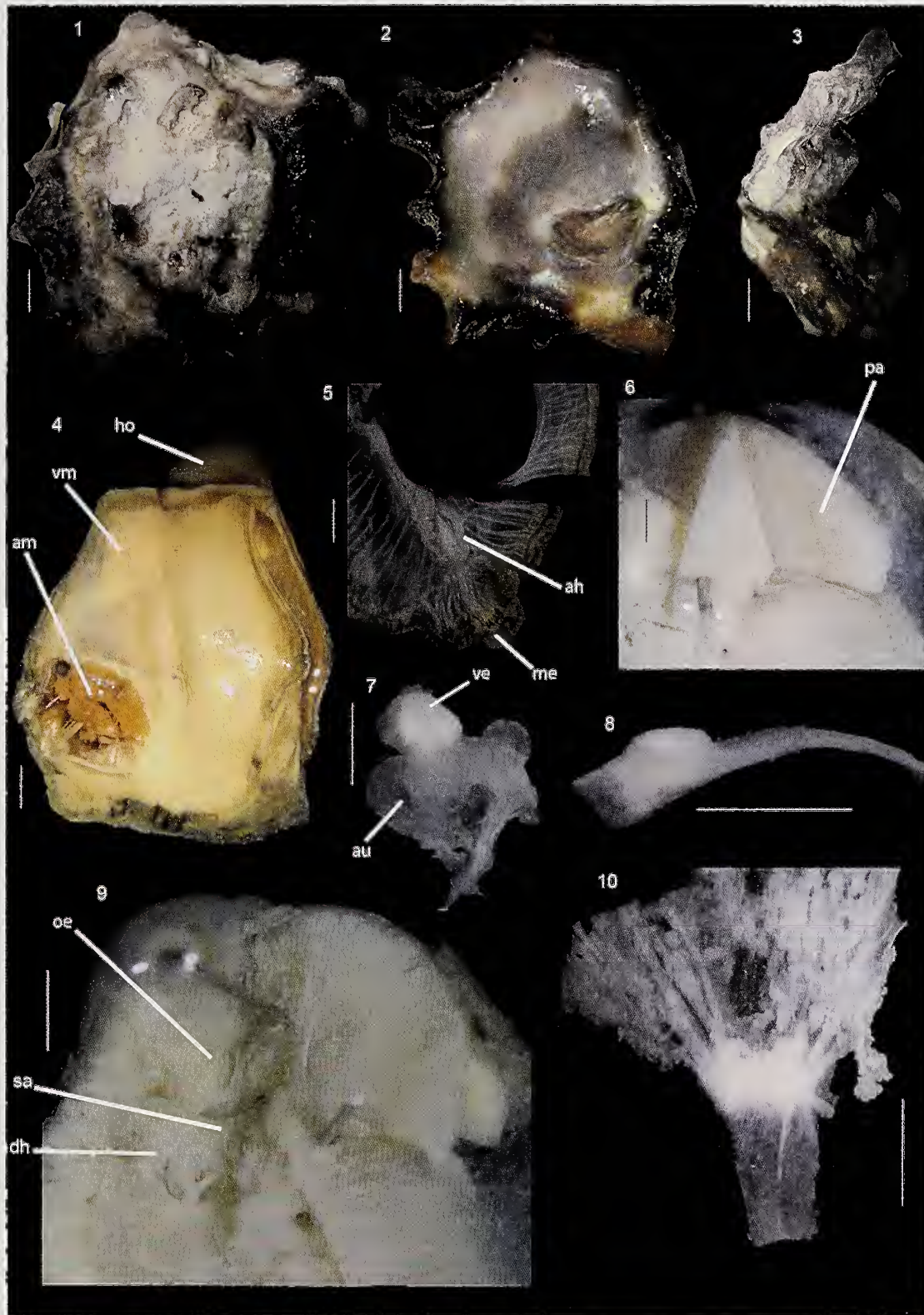
Lophia cornucopiae: Röding, 1798: 169.

Ostrea gibbosa Lamarek, 1819: 209; Hanley, 1856: 301.

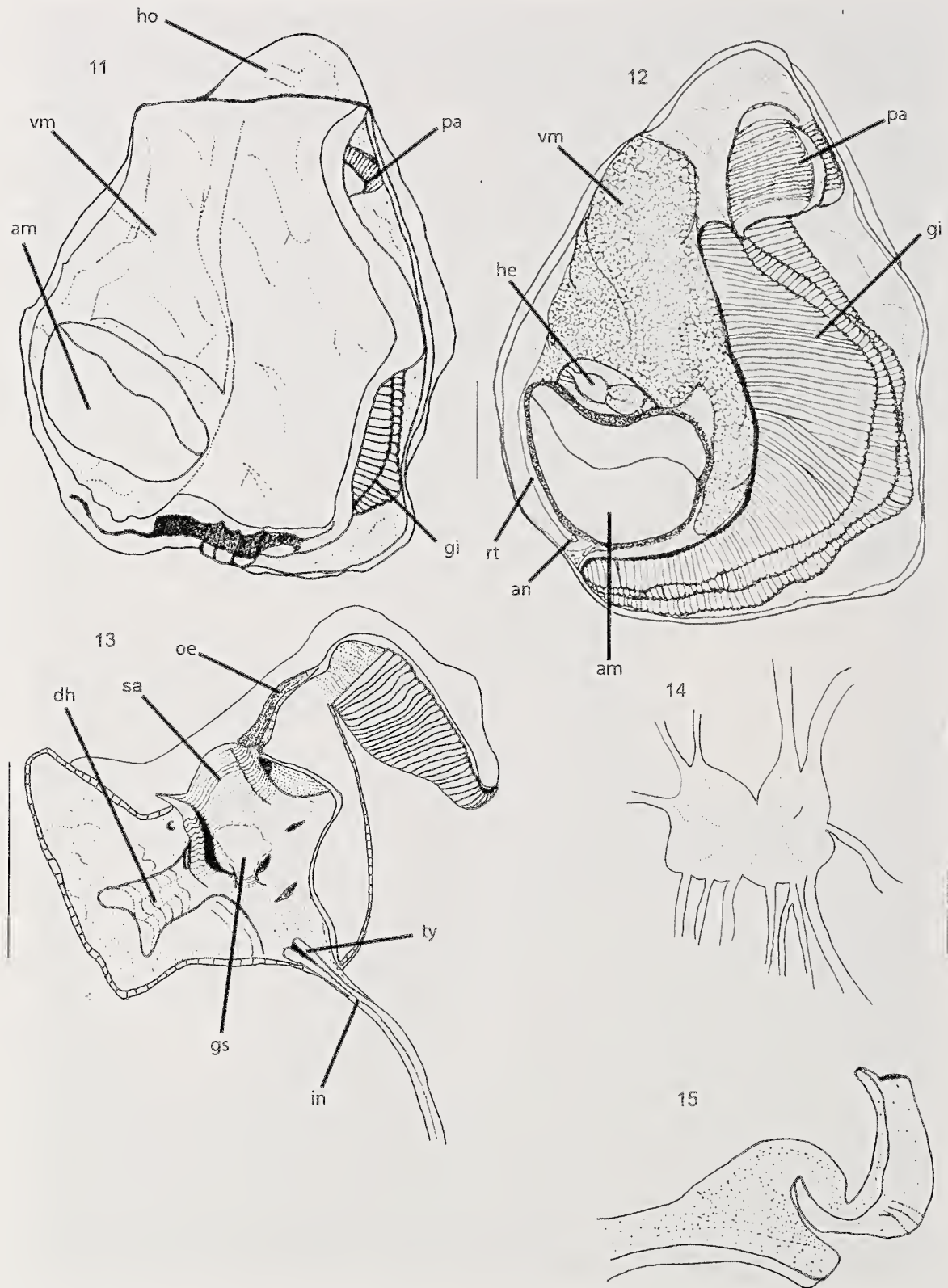
Crassostrea cucullata Ranson, 1960: 20.

Saccostrea cucullata: Stenzel, 1971: N1134–N1135, fig. J106; Morris, 1985: 125–128, Pl. 3, figs E–G; Lam and Morton, 2003: 110–112, pls. 11, 12; Lam and Morton, 2009: 482, fig. 1: 483.

Description: **SHELL:** Elongated, generally cup-shaped, to 100 mm. Right (upper) valve flat or slightly convex (Figure 2). Ligament alivincular. Left valve fixed to substrate, cupped and larger than right valve. Umbonal cavity of left valve. Margins of both valves with angles sculpture in the edge (Figures 1, 3); inner edge of right valve with small elongated denticles (Figure 2) producing corresponding depressions on left valve. Adductor muscle scar reniform, occupying $\frac{1}{4}$ of total shell height, in posterodorsal region (Figure 2), striate, white or grayish. Outside of valves variable from white to gray, light or dark brown, green or purple. Inner surface white, with occasional purple spots. **ADDUCTOR MUSCLE:** Reniform or slightly oval, located in posterior region, occupying $\frac{1}{4}$ of total soft part height (Figures 4, 11, 12). **MANTLE:** Mantle lobes thick, with well-defined pallial muscles, most abundant near adductor muscle (Figures 4, 5). Hood formed by junction of anterior mantle lobes. Hood robust and well-defined, usually free or filled by gonad mass (Figures 4, 11). **MANTLE EDGE:** Pleated and thick, dark, yellow with brown spots, bearing three similar-sized folds. Middle and inner folds with finger-like, uniformly distributed papillae, single or in pairs, with variable length (Figure 5). **GILLS:** Gills occupying 50% of total height. Demibranchs moderately thick, $\sim 1/3$ as thick as gill fold (Figures 6, 12). **CIRCULATORY SYSTEM:** Ventricle large, thick-walled, with internal beams crossing each other in various directions; opaque white. Outer part of auricles thin, translucent, trabecular; external portion of auricles bearing small, saculiform structures (Figure 7). Pair of kidneys triangular, tubular, mottled by light brown marks. Each kidney having direct communication with pericardium and gonad on medial side and communicating laterally by short chamber. Renal opening located on opposite side of cerebro-visceral connective. **DIGESTIVE SYSTEM:** Palps large, length $\frac{1}{4}$ of gill size, spatuliform; internal surface with pleats extending transversely to edge (Figure 6). Stomach in globular region of visceral mass, typically occupying $\frac{1}{4}$ of total length. Esophagus short, $\frac{1}{2}$ of palp length, (Figure 13). Sorting area of stomach (sa) short ($\frac{1}{2}$ of palp length) and wide with typhlosole beginning in posterior region of stomach (Figure 9, 13). Intestine separated from style sac, returning in opposite direction, passing usually behind pericardium, immersed in gonads; narrowest portion of intestine surrounding adductor muscle. Rectum long and thin, surrounding adductor muscle almost until canopy-gill junction. Anus sessile, rounded, $\frac{1}{2}$ of height of adductor muscle, with single fold. **REPRODUCTIVE SYSTEM:** Gonad composed of two lobes of follicular aspect, occupying $\frac{1}{4}$ of total animal size. Dorsally and ventrally spread in left lobe and right lobe; shape indistinct from each other. Two pairs of separate systems of genital channels, same as described above (excretory system). **NERVOUS SYSTEM:** Nervous system similar to other ostreid species. Pair of



Figures 1–10. *Saccostrea cucullata*, shell and anatomical features. **1.** Shell in right view. **2.** Right valve, internal view. **3.** Shell in ventral view. **4.** Complete soft parts; (ho) hood; (vm) visceral mass; (am) adductor muscle. **5.** Dissected mantle lobe, mantle edge and accessory heart; (ah) accessory heart; (me) mantle edge. **6.** Palps (pa), right-slightly ventral view, outer right hemipalp deflected. **7.** Heart isolated, showing ventricle (ve) and auricles (au). **8.** Anus and rectum. **9.** Anterior region, right view, digestive system exposed; (oe) esophagus; (sa) selection area; (dh) dorsal hood. **10.** Visceral ganglia, ventral view, adjacent layer of tissues also shown. Scale bars = 1 cm.



Figures 11–15. *Saccostrea cucullata*, anatomical features. **11.** General view of soft parts; (ho) hood; (vm) visceral mass; (pa) palps; (am) adductor muscle; (gi) gills. **12.** General view, right mantle lobe removed; (vm) visceral mass; (pa) palps; (am) adductor muscle; (gi) gills; (he) heart; (rt) rectum; (an) anus. **13.** Stomach, right view, opened longitudinally; (oe) esophagus, (sa) selection area, (dh) dorsal hood, (gs) gastric shield, (ty) typhlosole, (in) intestine. **14.** Visceral ganglia, ventral view. **15.** Detail of anus. Scale bars = 1 cm.

cerebral ganglia in anterior region, near palps; link at pair of visceral ganglia by connectives; visceral ganglia occupying 1/15 of adductor muscle area, with two pairs of branches in anterior region, three in posterior region and one laterally (Figures 10,14).

Type Material: Born's holotype is located at the Naturhistorisches Museum Vienna (Morris, 1985). *Ostrea cornucopiae*, Syntypes, Genève Museum n° 1089141, Lamarck Coll. (examined).

Material Examined: **CHINA:** Hong Kong, North Pacific Ocean, USNM 858434, 3 specimens; **NEW ZEALAND:** South Pacific Ocean, USNM 886486, 5 specimens; **THAILAND:** Chantaburi, Kung Kraben Bay, MZUSP 55270, (L. R. Simone coll. 24/vii/2005), 6 specimens.

Distribution: Indo-West Pacific.

***Saccostrea glomerata* (Gould, 1850)**
(Figures 16–27)

Ostrea glomerata Gould, 1850: 346; 1852: 462; Sowerby, 1871: sp. 64.

Ostrea attenuata Sowerby, 1871: pl. 21.

Ostrea vitrefacta Sowerby, 1871: sp. 80; Lamy, 1929: 166; Île-Rodriguez, 1938: 289.

Ostrea mordax.—Hutton, 1873b: 84 (*non* Gould, 1850).

Lopha glomerata.—Finlay, 1928: 268.

Ostrea forskali var. *glomerata*.—Lamy, 1929: 158.

Ostrea (Lopha) glomerata.—Hiro, 1936: 36; Wada, 1942: 70.

Crassostrea cucullata.—Ranson, 1967: 188; Nishimura et al., 1998: 85 (*non* Born, 1778).

Saccostrea glomerata.—Torigoe, 1981: 310, 332; Dinamani, 1991a: 335; Xu, 1997: 94.

Saccostrea cucullata.—Oliver, 1992: 88; Nishimura et al. 1998: 86, 88 (*non* Born, 1778).

Description: SHELL: Rounded, to 50 mm; left valve concave, slightly larger than right valve, lacking well-developed umbonal cavity (Figure 16). Right valve slightly convex; ligament short, with mild bulging in central region (Figure 17); margins of both valves with well-developed angles (Figures 16, 17); color internally dark brown at edges, fading toward median region of shell. Right valve with single row of rounded denticles spread along entire edge (Figure 17), with corresponding depressions on left valve. Adductor muscle scar reniform, occupying 1/5 of total inner shell area, located in median region, with anterior portion normally pigmented gray/brown and posterior portion with pigmented lines; surface slightly pearlescent, white-colored. Quenstedt muscle scar rounded, occupying 1/20 of total area of adductor muscle scar, located in anterior-ventral region of valves (Figure 17). MUSCLES: Adductor muscle reniform, occupying 1/3 of total height, with a convexity in posterior region (Figures 18, 24). MANTLE: Mantle lobes slightly thick, with well-defined pallial muscles more abundant near adductor muscle (Figures 18, 19). Mantle edge thick, reddish; middle fold with 3–4 short to long, elongated papillae; internal fold with

short to medium papillae, presenting 2–3 medium papillae for each short one (Figure 19). GILLS: Gills occupying ½ total body size. Alimentary channel narrow, ~1/5 as thick as gill fold (Figure 18). HEART: Heart well-developed. Ventricle relatively large, with internal bundles crossing each other in different directions, light beige. Auricles thin, with more abundant bundles, same texture, and coloration, but more elongated than ventricle (Figure 21). DIGESTIVE SYSTEM: Palps occupying ~1/5 of visceral mass, spatuliform, rounded; internal surface with plicae extending transversely to edge (Figures 20, 23, 25). Esophagus long and narrow; length ~1/2 of palp length (Figures 22, 26). Selection area (sa) long and thin, with typhlosoles beginning in posterior region of stomach (Figures 22, 26). Intestine passing behind pericardium, with narrowest portion surrounding adductor muscle. Rectum slightly long and thin, contouring adductor muscle at dorsolateral region. Anus with single fold (Figure 22). NERVOUS SYSTEM: Two pairs of branches in the anterior region and three in posterior region (Figure 27).

Type Material: Holotype, USNM 5960 (examined); Paratypes USNM 612314, MCZC 178590, 178591.

Material Examined: **Fiji:** Nanuya-Lailai Island, Yasawa Group T. Moala. MZUSP 71454; 2 specimens.

Distribution: India to Australia and New Zealand.

***Saccostrea echinata* (Quoy and Gaimard, 1835)**
(Figures 28–42)

Ostrea mytiloides Lamarck, 1819: 207; Deshayes, 1836: 227; Hanley, 1856: 300; Hidalgo, 1905: 387; Lamy, 1924: 155, 1929: 138 (*non* Gmelin, 1791).

Ostrea echinata Quoy and Gaimard, 1835: 455; Hanley, 1856: 302; Küster, 1868: 76; Hidalgo, 1905: 387; Chen et al. 1980: 174.

Ostrea arakanensis Sowerby, 1871: sp. 83.

Ostrea nigromarginata Sowerby, 1871: sp. 85; Lamy, 1928: 140.

Ostrea cucullata.—Pilsbry, 1895: 146 (*non* Born, 1778).

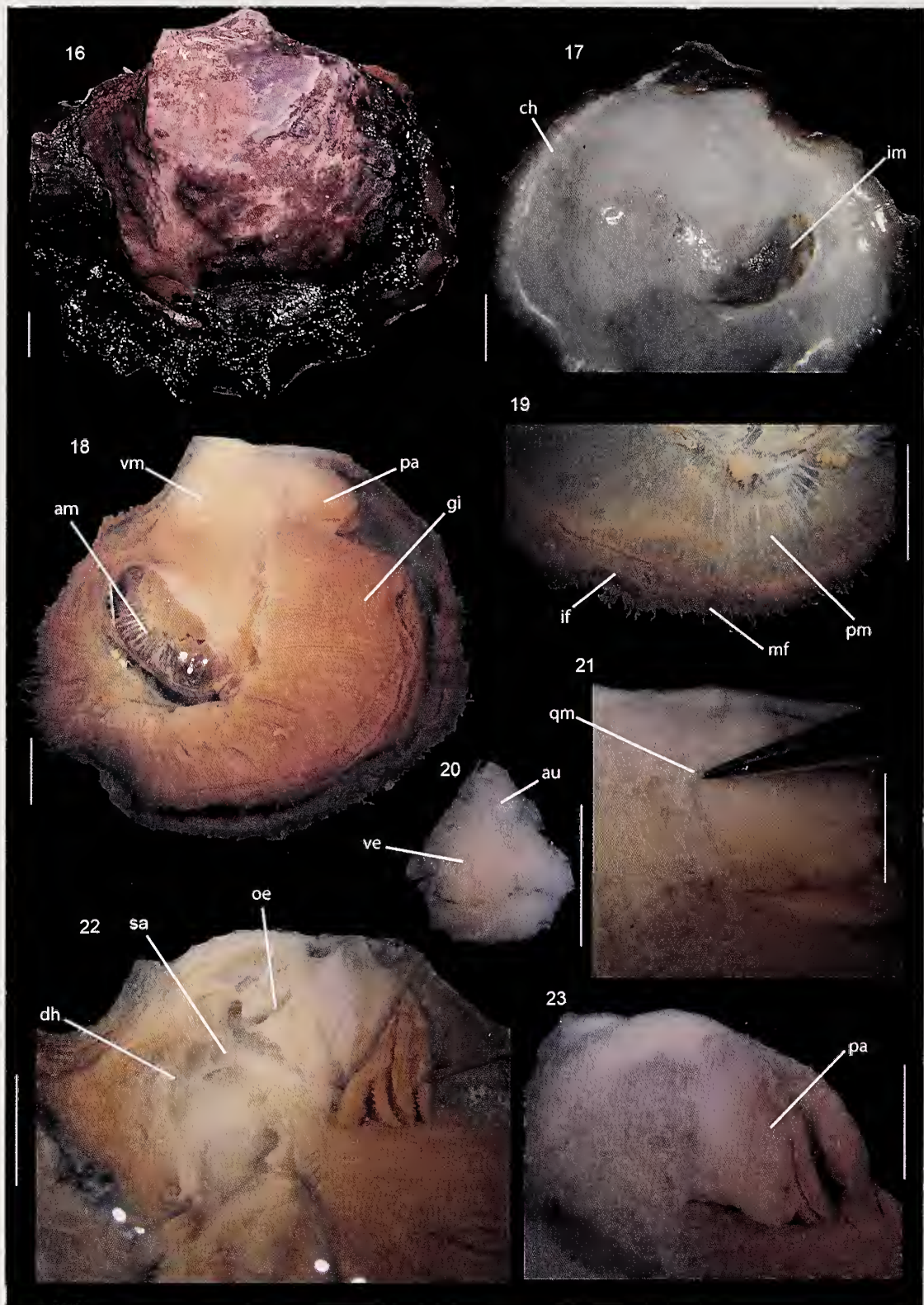
Crassostrea echinata.—Thompson, 1954: 152; Carreon, 1969: 113.

Saxostrea mytiloides [sic].—Habe and Kosuge, 1966: 145 (*non* Gmelin).

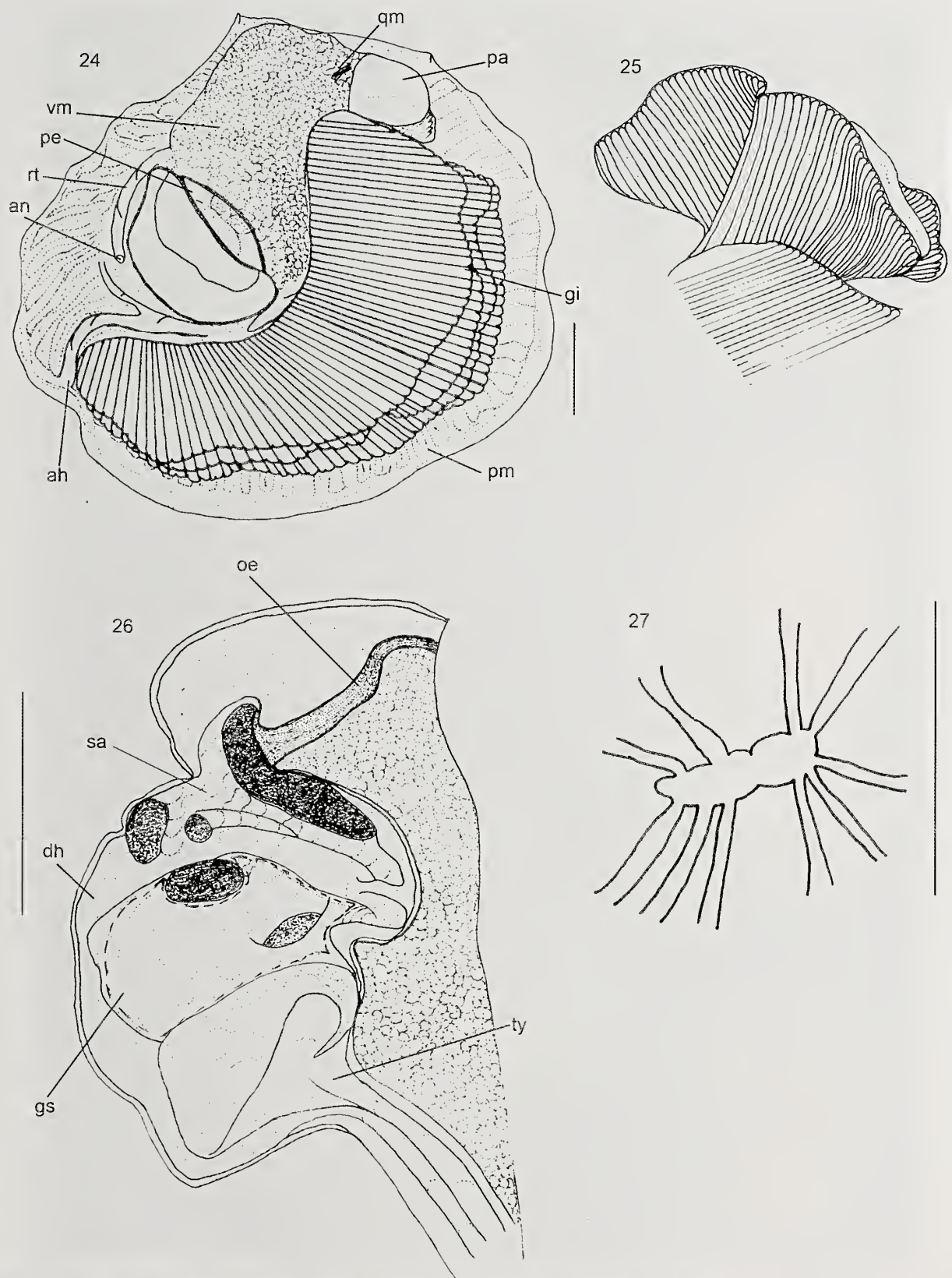
Saccostrea echinata.—Stenzel, 1971: N962; Torigoe and Inaba, 1981: 126; Torigoe, 1981: 308, 330; Li and Qi, 1994: 171; Hayami, 2000: 927.

Saccostrea cucullata.—Morris, 1985: 125; Harry, 1985: 150; Oliver, 1992: 88, 91; Xu, 1997: 95 (*non* Born, 1778).

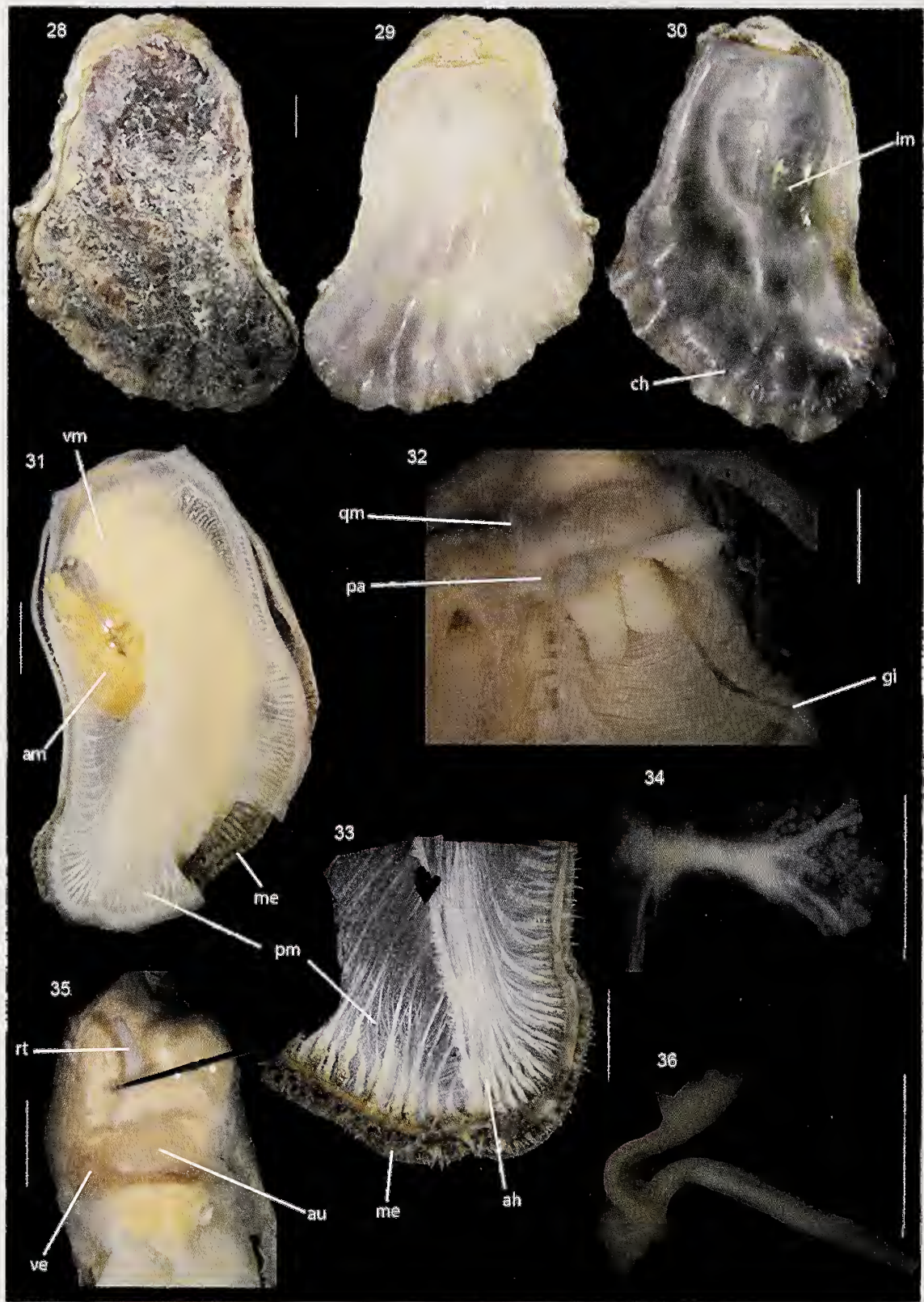
Description: SHELL: Elongated, ~ 60 mm, with slight ripples in margin of valves extending toward central region (Figures 28–30); left valve slightly larger than right valve, with deep umbonal cavity, lacking any major projections (Figure 29); internal color white/cream to gray. Adductor muscle scar elongate-reniform, occupying ~¼ of total height of shell, non-pigmented (Figure 30). Denticles present across edge of right valve (Figure 30),



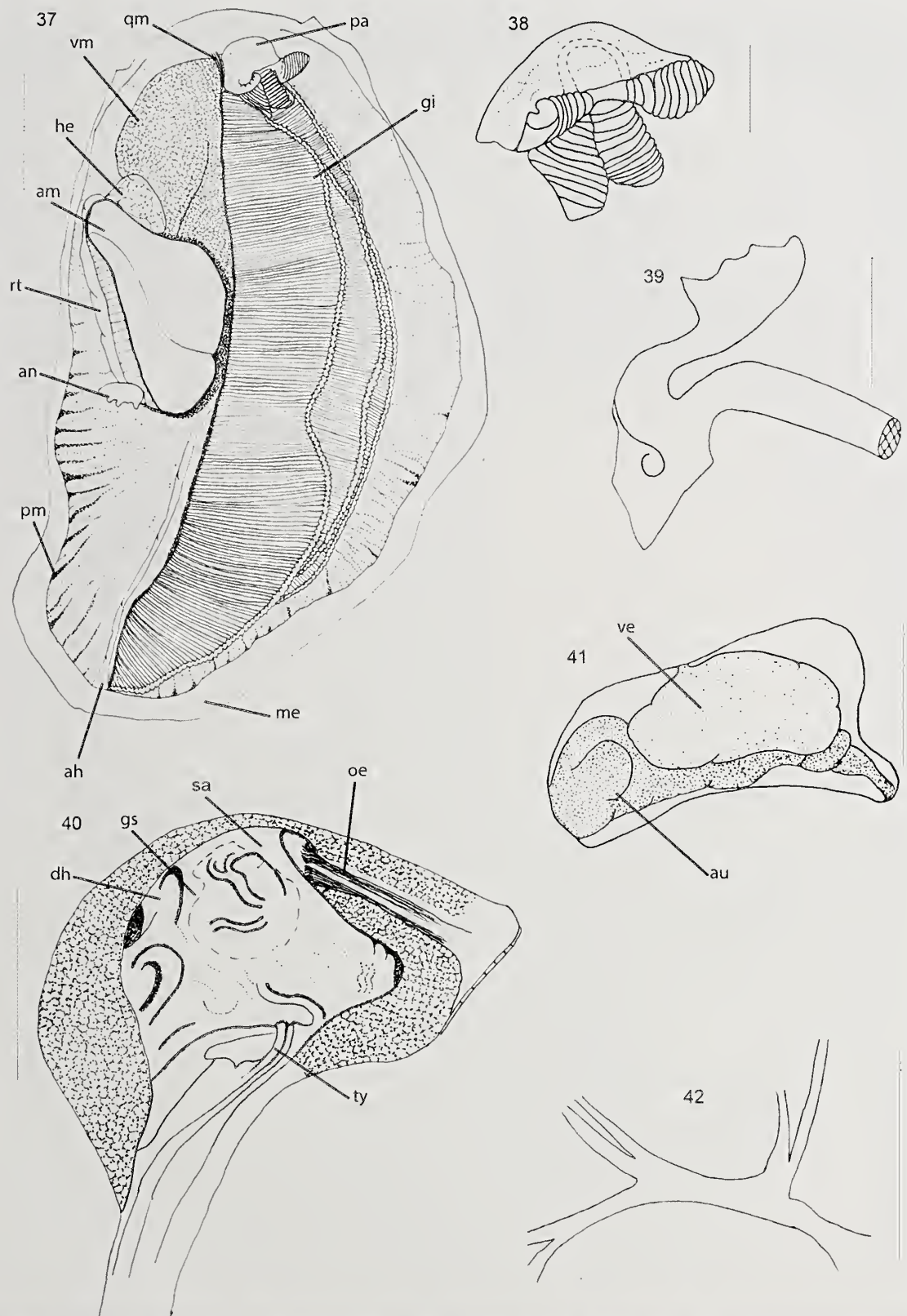
Figures 16–23. *Saccostrea glomerata*, shell and anatomical features. **16.** General right view. **17.** Right valve, internal view; (ch) chomata, (im) muscle impression. **18.** General view of soft parts right view, right mantle lobe removed; (vm) visceral mass, (am) adductor muscle, (pa) palps, (gi) gills. **19.** Mantle lobes and edge; (if) inner fold; (mf) middle fold; (pm) pallial muscles. **20.** Heart, ventral view; (ve) ventricle; (au) auricle. **21.** Anterior region, (qm) Quenstedt muscle. **22.** Anterior region, right view, with Stomach opened longitudinally; (oe) esophagus, (sa) selection area, (dh) dorsal hood. **23.** Palps (pa), right-slightly ventral view. Scale bars = 1 cm.



Figures 24–27. *Saccostrea glomerata*, anatomical features. **24.** General right view of soft parts; (qm) Quenstedt muscle, (pa) palps, (gi) gills, (pm) pallial muscles, (ah) accessory heart, (an) anus, (rt) rectum, (pe) pericardium, (vm) visceral mass. **25.** Detail of palps. **26.** Stomach opened longitudinally, right view; (oe) esophagus, (sa) selection area, (dh) dorsal hood, (ty) typhlosole. **27.** Visceral ganglia. Scale bars = 1 cm.



Figures 28–36. *Saccostrea echinata*, shell and anatomical features. 28. External view. 29. Internal view, left valve; (im) muscle impression; (ch) chomata. 30. Internal view right valve. 31. General view of soft part; (vm) visceral mass, (am) adductor muscle, (me) mantle edge. 32. Anterior region; (qm) Quenstedt muscle, (pa) palps, (gi) gills. 33. Mantle edge (me), detail of pallial muscles (pm) and accessory heart (ah). 34. Visceral ganglia. 35. Heart, (ve) ventricle, (au) auricle and rectum (rt). 36. Anus with expansion and rectum. Scale bars = 1 cm.



Figures 37–42. *Saccostrea echinata*, anatomical features. **37.** General view of soft parts; (qm) Quenstedt muscle, (vm) visceral mass, (he) heart, (am) adductor muscle, (rt) rectum, (an) anus, (pm) pallial muscles, (ah) accessory heart, (me) mantle edge, (gi) gills, (pa) palps. **38.** Palps, detail of median fusion of external hemipalps. **39.** Anus (an) and rectum (rt), detail of expansion in anus. **40.** Stomach, right view; (oe) esophagus, (sa) selection area, (gs) gastric shield, (dh) dorsal hood, (ty) typhlosole. **41.** Heart in pericardium; (ve) ventricle, (au) auricle. **42.** Visceral ganglia. Scale bars = 1 cm.

with corresponding depressions on left valve (Figure 29), distributed in various rows along posterior region, being elongated, rounded or both. **MUSCLES:** Reniform, occupying $\sim 1/4$ of total height, with a convexity in posterior region (Figures 30, 37). **MANTLE:** Mantle edges delicate, with well-defined pallial muscles in all mantle surfaces. Hood filled with gonads (Figures 31, 33, 37). **MANTLE EDGE:** Mantle edge thick, with yellow and/or brown pigmentation. Papillae of middle fold alternately long and short; usually with a long papilla for each three short ones. Accessory heart with only one branch on both lobes, thin and translucent; lobes not reaching adductor muscle (Figure 33). **GILLS:** Gills occupying $1/2$ of total height. Alimentary chamber thick, $\sim 1/2$ as thick as gill fold (Figures 32, 37). **CIRCULATORY SYSTEM:** Ventricle thin, usually translucent, auricles elongated, less cross-linked, non-pigmented (Figures 35, 41). **DIGESTIVE SYSTEM:** Palps small, $\sim 1/4$ of adductor muscle size, curved, sickle-shaped, with folds along anterior margin. External palps fused in middle region and overlying internal palps (Figures 32, 39). Esophagus long ($\sim 1/3$ of adductor muscle) and thin. Selection area of stomach (sa) short ($\sim 1/2$ of esophagus size) and wide, with typhlosole (ty) beginning in posterior region of stomach (Figure 38). Intestine passing behind pericardium; narrowest portion circling adductor muscle. Rectum long and thin, girdling adductor muscle. Anus papillae shaped similarly to shell (Figure 35, 36, 40). **NERVOUS SYSTEM:** With three branches in anterior region and only one in posterior region (Figures 34, 42).

Type Material: Holotype in MNHN (examined).

Material Examined: **MARIANA ISLANDS:** Guam, UF 284793; 3 specimens.

Distribution: E. Africa to Japan.

***Saccostrea palmula* (Carpenter, 1857)**
(Figures 43–53)

Ostrea palmula Carpenter, 1857b: 163, 550; 1864: 538; Dall, 1914: 2; Lamy, 1929: 150; Keen, 1971: 84; Abbott, 1974: 456.

Ostrea plumula [sic].—Carpenter, 1857b: 351, 353.

Ostrea amara Carpenter 1864a: 363; 1864: 541, 552, 621, 666; Lamy, 1930: 242.

Ostrea frons.—Carpenter, 1864: 520 (*non* Linnaeus, 1758).

Ostrea mexicana Sowerby, 1871: sp. 35.

Ostrea cumingiana var. *Mexicana*.—Dall, 1914: 2.

Ostrea conchaphila (pars).—Abbott, 1974: 456 (*non* Carpenter, 1857).

Saccostrea palmula.—Harry, 1985: 138.

Crassostrea palmula.—Rodríguez and García-Cubas, 1986: 269.

Description: **SHELL:** Shell rounded, to ~ 60 mm. Left valve larger than right valve, with small umbonal cavity and slight projection in ligament region; projections and evident ripples present along margin (Figures 43, 44). Right valve smaller than left valve, opercular, following

pattern of expansion of left valve (Figure 44). Color white/cream with purple spots on outer surface; inner surface white, slightly nacreous, with occasional purple spots and lines. Adductor muscle scar well-defined, showing purple concentric lines in anteroventral portion of valves, reniform (Figures 44, 45), occupying $1/5$ of total height. Denticles rounded in anterior region, aligned, uniformly distributed; corresponding depressions on right valve shallow, almost inconspicuous (Figure 44). **MUSCLES:** Same morphology as other species, reniform (Figures 46, 47, 50), occupying $\sim 1/5$ of total height. **MANTLE:** Mantle lobes thin, with well-defined pallial muscles in posterior region (Figures 46, 50); hood absent. Mantle edge thinner, beige to cream; middle fold bearing two to five finger-like, medium papillae for each two long ones (Figure 47). Accessory heart with three well-defined branches, reaching and circling adductor muscle in ventral region (Figure 47). **GILLS:** Gills occupying $\sim 1/3$ of total body size. Alimentary chamber narrow (Figures 46, 48). **HEART:** Ventricle elongated, slightly thick, reticulated and whitish. Auricles thin, small and non-pigmented (Figures 46, 50). **DIGESTIVE SYSTEM:** Palps large, occupying half as large as adductor muscle, thin, with folds on upper margin (Figures 48, 51).

Nervous System: Visceral ganglia with two anterior expansions, two lateral and tree posterior ones (Figures 49, 53).

Type Material: Syntypes, BMNH 1857.6. 4.735, 1857.6. 4.736, 1857.6. 4.737 (examined).

Material Examined: **PANAMA:** Miraflores Lock, USNM 734199, 2 specimens; Arraijan, FMNH 27226, 2 specimens.

Distribution: Mexico to Peru.

***Saccostrea mordax* Gould, 1850**
(Figures 54–64)

Ostrea mordax Gould, 1850: 346; 1852: 464; 1856: pl. 43; Sowerby, 1871: sp. 31; Saville-Kent, 1891: 2; 1892: 65, 245; Hutton, 1937b: 84; Hirase and Taki, 1951: pl. 7.

Ostrea cornucopiae Saville-Kent, 1891: 3 (*non* Gmelin, 1791).

Ostrea mordax var. *cornucopiaeformis* Saville-Kent, 1893: 248.

Ostrea cucullata.—Iwakawa, 1915: 15; 1919: 254; Hatai, 1941: 58; Wells and Bryce, 1988: 162.

Ostrea forskali var. *sueli* Lamy, 1925: 192.

Ostrea (Lopha) cucullata.—Kuroda, 1928: sp. 36; Hirase, 1930: 25; 1934: 5; Takatsuki, 1949: 5 (*non* Born, 1778).

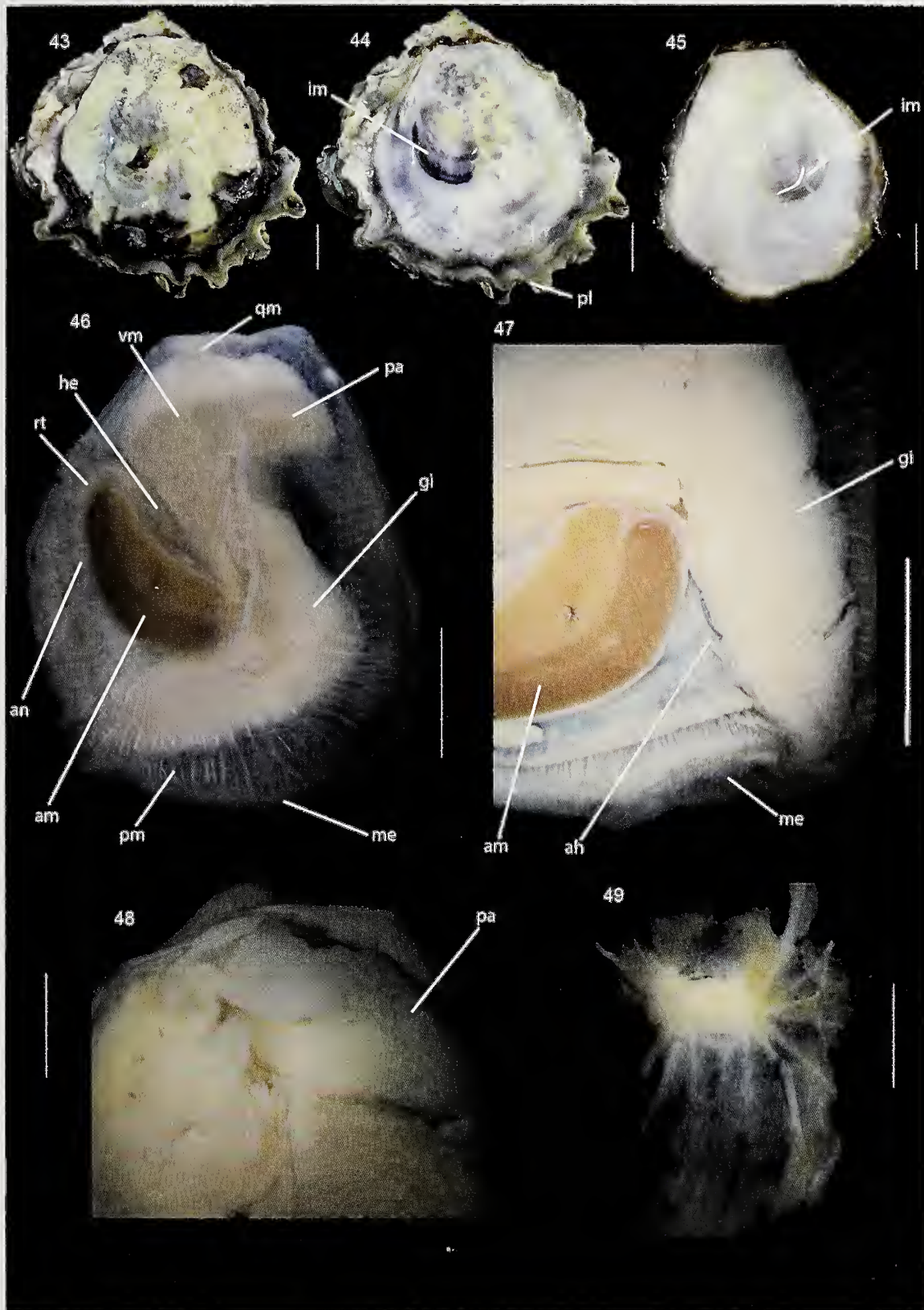
Ostrea forskali var. *mordax*.—Lamy, 1929: 158.

Ostrea (Lopha) mordax.—Kuroda, 1930: 51; Tchang and Lo, 1956: 74.

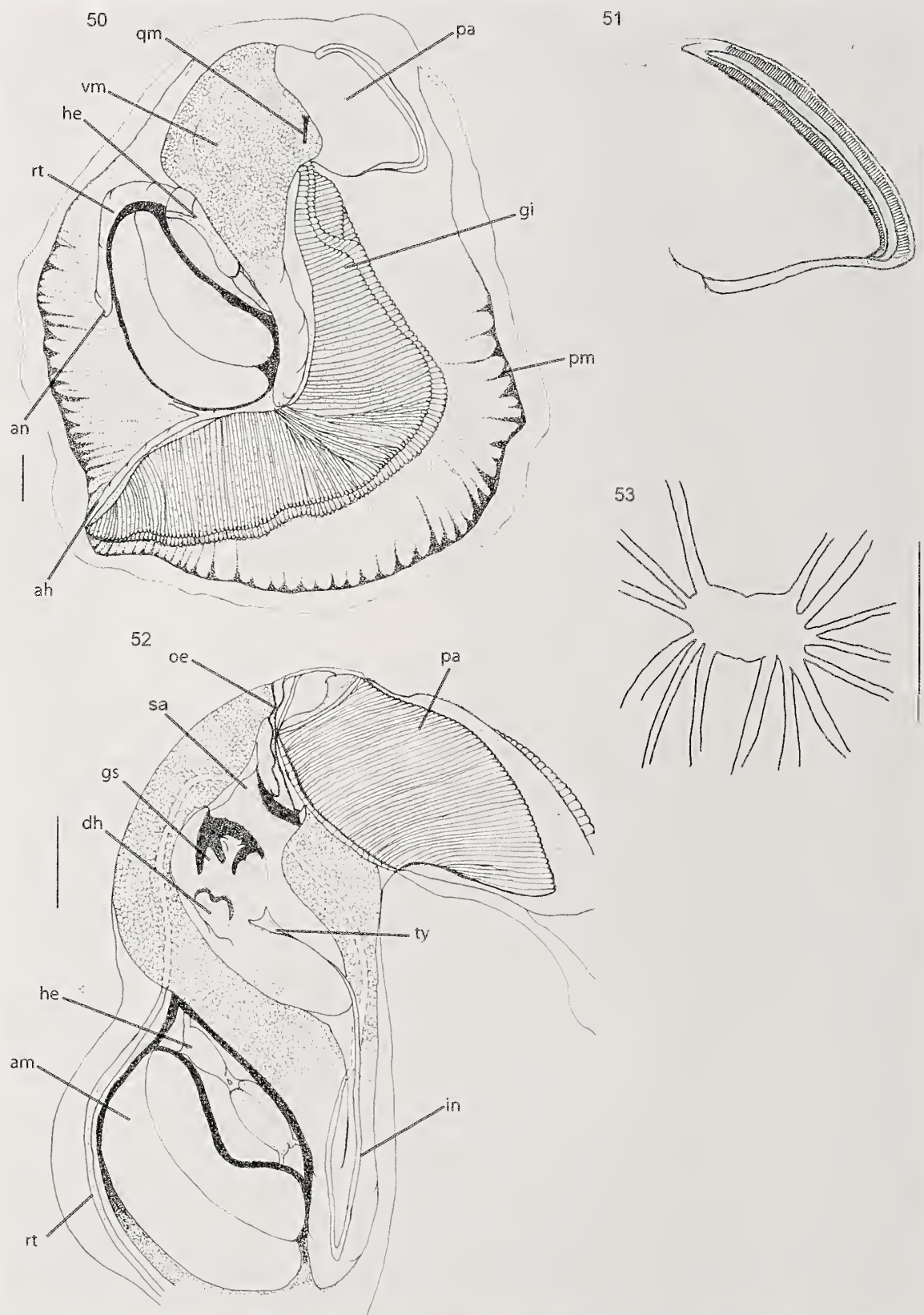
Saxostrea amasa Iredale, 1939: 399; Allan, 1959: 273.

Ostrea glomerata.—Blanco et al., 1951: 52 (*non* Gould, 1850).

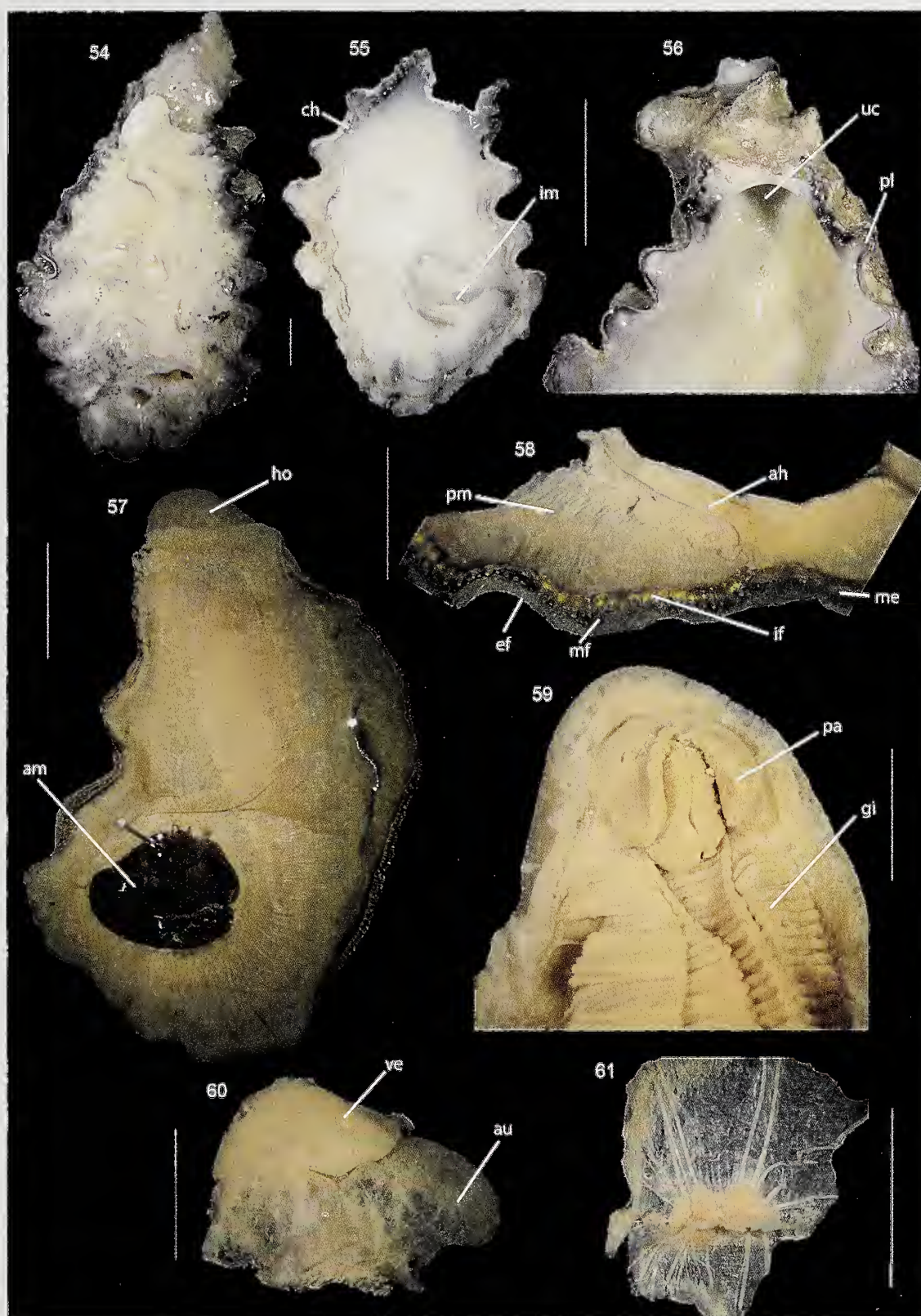
Crassostrea amasa.—Thompson, 1954: 154; Carreon, 1969: 111.



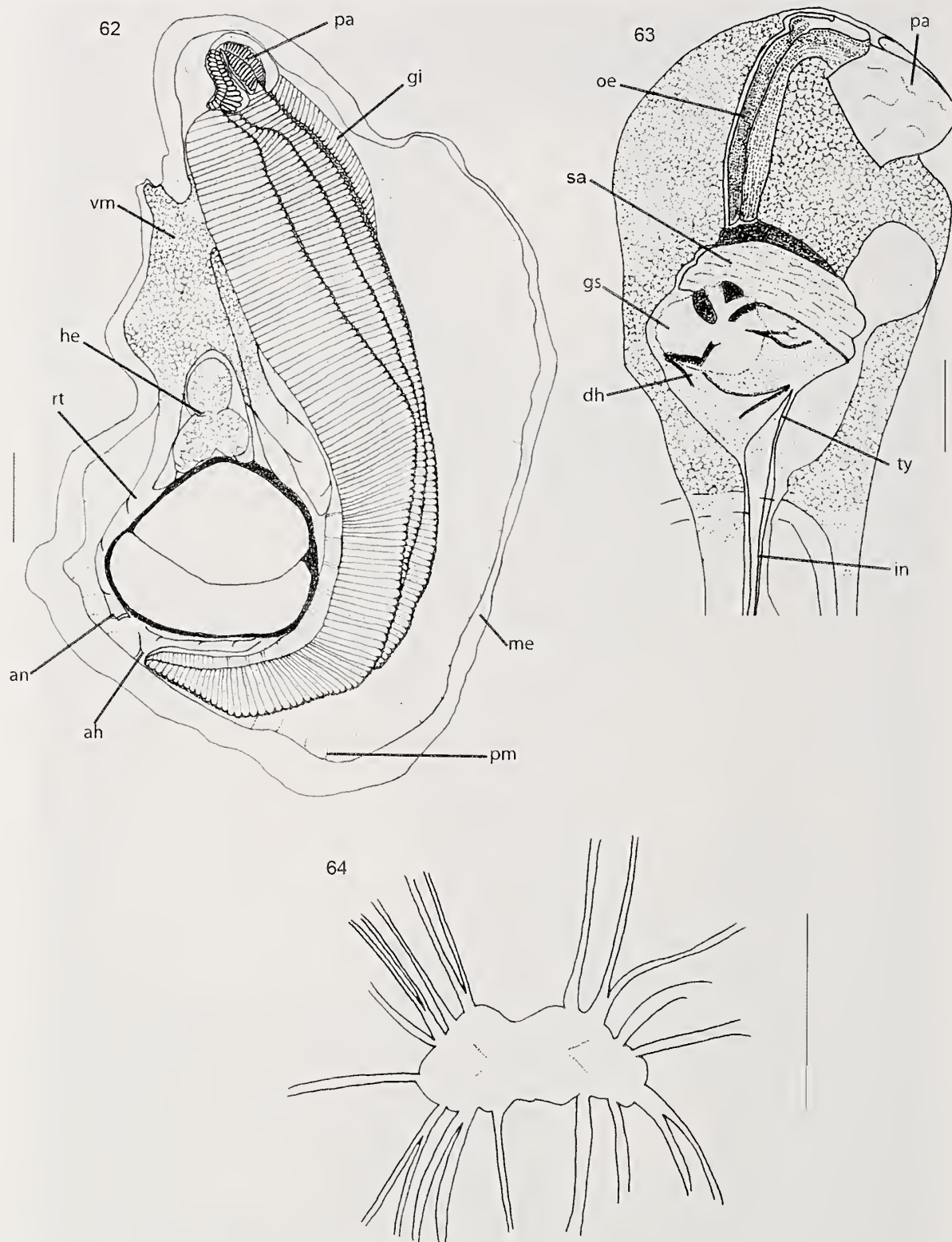
Figures 43–49. *Saccostrea palmula*, anatomical features. **43.** External view. **44.** Internal view of left valve, (im) muscle impression. **45.** Internal view of right valve. **46.** General view of soft parts; (qm) Quenstedt muscle, (vm) visceral mass, (he) heart, (rt) rectum, (an) anus, (am) adductor muscle, (pm) pallial muscles, (me) mantle edge, (gi) gills, (pa) palps. **47.** Posterior region, detail for a gills (gi), mantle edge (me), accessory heart (ah) and adductor muscle (am). **48.** Detail of palps. **49.** Visceral ganglia. Scale bars = 1 cm.



Figures 50–53. *Saccostrea palmula*, shell and anatomical features. **50.** General view of soft parts; (qm) Quenstedt muscle, (vm) visceral mass, (he) heart, (rt) rectum, (an) anus, (ah) accessory heart, (pm) pallial muscles, (gi) gills, (pa) palps. **51.** Detail of palps. **52.** Stomach, right view; (oe) esophagus, (sa) selection area, (gs) gastric shield, (dh) dorsal hood, (ty) typhlosole, (pa) palps, (he) heart, (am) adductor muscle, (rt) rectum, (in) intestine. **53.** Visceral ganglia. Scale bars = 1 cm.



Figures 54–61. *Saccostrea mordax*, shell and anatomical features. **54.** External view. **55.** Internal view of right valve; (ch) chomata, (im) muscle impression. **56.** Internal view of left valve, detail of undulations (pl) of the edge valves and umbonal cavity (uc). **57.** General view of soft part; (ho) hood, (an) anus. **58.** Mantle edge, detail of accessory heart (ah) and pallial muscles (pm); (ef) external fold, (mf) middle fold, (if) inner fold, (me) mantle edge. **59.** Detail of the palps (pa) and gills (gi). **60.** Heart; (ve) ventricle, (au) auricle. **61.** Visceral ganglia. Scale bars = 1 cm.



Figures 62–64. *Saccostrea mordax*, anatomical features. **62.** General view of soft parts; (pa) palps, (gi) gills, (vm) visceral mass, (he) heart, (rt) rectum, (an) anus, (am) adductor muscles, (pm) pallial muscles, (me) mantle edge. **63.** Stomach, right view; (pa) palps, (oe) esophagus, (sa) selection area, (gs) gastric shield, (dh) dorsal hood, (ty) typhlosole, (in) intestine. **64.** Visceral ganglia. Scale bars = 1 cm.

Saxostrea mordax.—Habe, 1951: 94; Kira, 1959: 127; 1962: 144; Taki, 1960: 192; Habe and Kosuge, 1966: 145; 1967: 137.

Saccostrea mordax.—Habe and Okutani, 1975: 194; Habe, 1977: 109; 1981: 83; Torigoe, 1981: 306, 328; Okutani and Soyama, 1987: 152; Habe and Matsuda, 1990: 98; Xu, 1997: 95; Hayami, 2000: 925.

Saccostrea cucullata —Morris, 1985: 125; Li and Qi, 1994: 170; Lamprell and Healy, 1998: 134 (*non* Born, 1778).

Description: SHELL: Shell elongated, to ~40 mm, with undulations on entire edge of both valves up to ligamentary region (Figure 54). Left valve concave, umbonal cavity well-developed, with extensive anterior projection (Figure 56). Right valve flat or slightly convex, not opercular (Figure 55). Color beige/cream, with edges of valves dark purple. Denticles present along edges; rounded, relatively large and distributed in single row (Figure 55). Adductor muscle scar oval, grayish or non-pigmented (Figure 55). MANTLE: Mantle thick, with pallial muscles more evident in adductor muscle region. Hood present, robust, filled by gonads and palps (Figure 57). Mantle edge thin, dark brown and yellow; middle fold with small and medium finger-like papillae; 2–4 small papillae for each larger one. Internal fold with small, uniformly distributed finger-like papillae. Accessory heart inverse-T shaped, well-marked, and surrounding ventral region of adductor muscle (Figures 58, 62). GILLS: Gills occupying ~½ of total area. Alimentary chamber narrow (Figures 59, 62). CIRCULATORY SYSTEM: Ventricle large, ~2/3 as large as auricles, with slight bundles more concentrated in posterior region; whitish. Auricles elongated, translucent (Figure 60). DIGESTIVE SYSTEM: Palps large and thick, ~½ of adductor muscle size, superior edge with folds; external palps covers ~1/3 of internal palps (Figures 59, 62). Esophagus long, twice as long as palps. Selection area of stomach (sa) long and narrow, ½ as high as esophagus; typhlosole in terminal region of globular portion (Figure 63). NERVOUS SYSTEM: Visceral ganglia with tree nerves in anterior and posterior region and one laterally (Figures 61, 64).

Type Material: Syntype, NMNH 5958 (examined).

Material Examined: CHINA: Taiwan, Taipei Co., Wanli, Yehliu, UF 303012, 3 specimens.

Distribution: Indo-West Pacific.

DISCUSSION

It is an accepted fact that the taxonomy of *Saccostrea* is problematic because of shell plasticity (Lam and Morton, 2006). Still, except for the shell, the anatomy of the species is mostly unknown (e.g., Lam and Morton, 2004, 2006, 2009). Among the species studied here, the only one with a described anatomy was *S. cucullata*, by Awati and Rai (1931).

The shell of *Saccostrea* differs from that of *Crassostrea* basically by the presence of chomata and the ornamentation of the edge in some species. Both genera have

medium to large-sized shells and occur in similar habitats, but *Saccostrea* species they were found only in the Pacific and Indian Oceans. An invasive species of the genus *Saccostrea*, found in São Sebastião (São Paulo, Brazil), is identified as *S. cucullata* (see Amaral and Simone, in press). As we demonstrate herein, among the *Saccostrea* species, taxonomy is problematic only when based solely on shell characters (even so, differences in shell morphology may be found when the characters are considered in sufficient detail). Anatomical characters are useful and sufficient for species-level identification. Methods in molecular systematics have been advocated as the only tools for identification of the various lineages of *Saccostrea* (Lam and Morton, 2006: 7). Observations of *S. mordax* suggest that it occurs only on exposed, wholly marine rocky shores, whereas other *Saccostrea* lineages occupy a wide range of habitats from brackish mangroves to somewhat less exposed marine shores (Lam and Morton, 2006).

Shell: The shells of *Saccostrea cucullata* are elongated, normally cup-shaped, with a deeply concave left valve showing an expansion in the ligament area. The right valve is flat or slightly convex, like a lid. The shell of *S. glomerata* is rounded, with a concave left valve slightly larger than the right valve, and a slightly convex right valve. In *S. echinata*, the shell is more elongated, with slight undulations, along the edge of the valves that stretch toward the central area. *S. palmula* has a rounded shell, with both valves laterally expanded; the left valve is larger than the right, and the right valve is small and opercular. *Saccostrea mordax* has a usually elongated shell, with undulations going from the margins to the ligament region; the left valve is concave, the right valve is almost flat or slightly convex, but it is not opercular as in the remaining species, and both valves have a similar width.

The shell edge undulations are characteristic of *Saccostrea*, with this character usually separating its species from those of *Crassostrea*. When present in *Crassostrea*, this undulation is only observed in the posterior region and in follicular layers.

The umbonal cavity is well-defined in *Saccostrea cucullata*, *S. echinata*, and *S. mordax*. In *S. glomerata* and *S. palmula* it is small or absent. According to Stenzel (1971: N995), the deepest umbonal cavities and the largest number of chambers are found in *Saccostrea*, particularly in the high-conical, rudist-like ecomorphs of the “living complex superspecies *S. cucullata*” from the tropical Indo-Pacific.

The shell edge in *S. cucullata* has small tubercles (elongated chomata). They are present along the inner edge of the right valve, with corresponding depressions on the left valve. In *S. glomerata*, the margins of both valves have well-developed angles; the right valve shows rounded chomata spread along its entire edge, arranged in single row, with corresponding depressions on the left valve. In *S. echinata*, the chomata are present along the right valve's edge, with corresponding depressions on the left valve; these chomata are distributed in multiple rows

in the posterior region, and may have an elongated or rounded contour. *Saccostrea palmula* has evident projections and undulations along the shell's edge; following the pattern of expansions of the left valve, both valves show more rounded chomata on the edge than those of *S. cucullata*, which is restricted to the anterior region, aligned and uniformly distributed. The corresponding depressions on the right valve are somewhat shallow. *Saccostrea mordax* has chomata along the edges on both valves; they are rounded, relatively large and distributed in a single row.

Some oysters have chomata distributed around the peripheries of their valves, including the valve margins directly opposed to the hinge. True teeth are never found in this area of bivalve shells. Chomata are not analogous to teeth or sockets. The genus *Saccostrea* has strongly developed chomata, tall and strong tubercles on the right, and deep pits on the left valves along the whole periphery of the valves (Stenzel, 1971).

In *Saccostrea cucullata*, the external surface of the valves is variable in color, from pale white, light-gray to dark-brown, greenish, or purple. The internal surface is white, and may present purple spots. These characteristics support those presented by Awati and Rai (1931). *Saccostrea glomerata* is internally colored dark brown at the edges, fading toward the median region of the shell. Comparatively, *S. echinata* is colored white/cream to grayish. *Saccostrea palmula* is colored white/cream with purple spots externally, and the internal surface is white and slightly nacreous; there may be purple spots in the region corresponding to the mantle edge on both valves. In *Saccostrea mordax*, color is cream in the middle, with dark purple colored in the internal margins.

The adductor muscle scar in *Saccostrea cucullata* is reniform, striated, white or grayish. In *S. glomerata*, the adductor muscle scar is reniform, occupying 1/5 of total area, located in the median region, with anterior portion normally pigmented gray/brown and a posterior portion with pigmented lines. Its surface is slightly opalescent and white. In *S. echinata*, the adductor muscle scar is also reniform but more elongated and unpigmented; in *S. palmula*, it differs from the above-mentioned species: the adductor muscle scar is defined by concentric purple lines in the anteroventral portion of the valves, but it is also reniform. *S. mordax* has an oval adductor muscle scar, grayish, with concentric lines that may be pigmented. These characteristics fit with those described by Lam and Morton (2009).

All species of *Saccostrea* exhibit a slight Quenstedt muscle scar, a rounded mark located in the anteroventral region of the valves. These imprints have been noticed on many oyster species, fossil and living (Dall, 1880; Hedman and Boyce, 1890; Stenzel, 1971; Harry, 1985).

The adductor muscle (and scar) of Crassostreinae in general do not differ among genera but show variations among species. These variations have been pointed out in the literature (Nascimento, 1991 for *C. rhizophorae*; Galtsoff, 1964 and Kennedy et al., 1996 for *C. virginica*),

and are possibly associated with the high level of shell plasticity.

Adductor Muscle: The adductor muscle is short and stout and directly connects the two valves. It is differentiated by its whole length into two coalescent subdivisions: the catch muscle (with opalescent and opaque color in live oysters, comprising the ventral or distal part of the muscle), and the quick muscle (flesh, colored and translucent, comprising the dorsal or proximal part of the muscle). The relative sizes of the two subdivisions differ among genera (Stenzel, 1971). *Ostrea* has a larger catch muscle than *Crassostrea* and *Saccostrea*; *Hyotissa* has the smallest one.

Saccostrea cucullata shows a normally reniform adductor muscle, which is sometimes oval while *S. palmula* has a strictly reniform muscle. *Saccostrea glomerata* has a reniform adductor muscle, with a convexity in the posterior region. *Saccostrea echinata* also has a reniform adductor muscle, but with a convexity toward the posterior region (that of *S. cucullata* is anterior). *Saccostrea mordax* has a strictly oval adductor muscle.

The Quenstedt muscles are a pair of tiny muscles, each attached at one extremity to a valve, and having the opposite extremity ending among the oral part of the gills. The pair of Quenstedt muscles has no differentiation regarding the origin on the shell and the insertion in the base of the palps in the five species. Galtsoff (1964), Stenzel (1971), and Mesquita (1993), observed that the Quenstedt muscles are difficult to find, but, according to Amaral and Simone (2014), the pair of Quenstedt muscles are visible when opening the valves in all species of Crassostreinae. From their origin on the shell, the muscles run through the anterior visceral mass up to the insertion in the base of the palps. This peculiar morphological arrangement shows no probable homology with the anterior adductor muscle or any foot muscles (Galtsoff, 1964; Stenzel, 1971).

Mantle: The mantle lobes of an adult oyster are thick and somewhat solid, having many muscles strands, some arranged in concentric and others in radial patterns (Stenzel, 1971). In *Saccostrea cucullata*, the lobes are thick, with well-defined pallial muscles, mainly around the adductor muscle; the hood is robust, well-defined, normally free or filled by gonads. In *S. glomerata*, the mantle is slightly thick, with pallial muscles more evident in the adductor muscle region, and the hood is absent. In *S. echinata*, the mantle lobes are thin, with well-defined pallial muscles along the mantle's extension. It has a smaller hood than *S. cucullata*. *Saccostrea palmula* has a thick mantle with pallial muscles more evident around the adductor muscle. The hood is not present. In *S. mordax*, the mantle lobes are thick with pallial muscles more evident in the adductor muscle region. It also has a well-defined hood, filled by gonads and palps. The pallial muscles show some differences among species, in quantity, girth, or location.

Saccostrea cucullata has a thick mantle edge, colored dark yellow with brown spots. Its three folds have similar size; the middle and inner folds also have finger-like papillae, one or two short for each long one. *Saccostrea glomerata* has a thick mantle edge with reddish color; the middle fold has both short and long papillae, at a ratio of three to four short for each long one; the inner fold has short and medium papillae, usually two or three medium for each short one. In *S. echinata*, the mantle edge is thick and colored yellow and/or brown; the papillae of the middle fold are alternately long and short, with three short for each long one. *Saccostrea palmula* has a thin edge, colored beige/cream; the finger-like papillae of the middle fold are small, elongated, alternately short and medium/long. Usually, two to five small papillae are present for each one or two long/medium ones. *S. mordax* has a thin edge, colored dark brown and/or yellow; the middle fold bears medium and short finger-like papillae, at a ratio of two to four short papillae for each medium one; the internal fold bears small, uniformly distributed finger-like papillae. This variation (size and distribution) was also found in Amaral and Simone (2014) for *Crassostrea* species.

The accessory heart in *Saccostrea cucullata* has three well-defined branches in the right lobe, forming a short y-shaped structure while the left lobe shows only a single large branch. In *S. echinata*, the accessory heart is slim, translucent, with thin walls, not reaching the adductor muscle in both lobes. In *S. palmula*, it has tree branches that contour the adductor muscle. *Saccostrea mordax* shows a different arrangement, forming a well-defined inverted T-shaped structure, and girdling the adductor muscle in the ventral region. *Saccostrea glomerata* has three branches in both lobes, forming a thick y-shaped structure, and one branch, about 1/3 thinner, which borders the adductor muscle.

Differently from the species described here, *Crassostrea* had tree branches in all studied species in Amaral and Simone (2014). This characteristic can be used as a distinction between *Saccostrea* and *Crassostrea*.

The promial passage was first reported by Kellogg (1892: 396–397). Nelson (1938) was the first to recognize its significance and to elucidate its function. The promial passage is present in all *Saccostrea*. This is a characteristic of the nonincubatory ostreid genera (e.g., *Crassostrea*, *Saccostrea*, *Striostrea*, *Hyotissa*, *Neopcygnodonte*; Stenzel, 1971). The promial passage varies in size: in species of *Crassostrea* it appears on both sides as a long chamber, from the margin of the visceral mass to the base of the gills; in *Saccostrea*, the passage is open only in the left lobe and open to half of length of the visceral mass.

Gills: The number of gill folds and filaments is very variable, apparently increasing proportionally to the animal's size. However, these numbers can vary among individuals of similar size. Ridewood (1903) mentioned 9–12 filaments per fold in *Ostrea edulis*, while Atkins (1937a) mentioned 8–17. Atkins (1937a) mentioned 8–17 in *Crassostrea virginica*; Nelson (1938) mentioned 8–15. Galtsoff (1964) mentioned 10–16 filaments per fold in

C. angulata, while Atkins (1937a) referred to 15–16 and Nelson (1938) 8–14 filaments per fold. Amaral and Simone (2014) observed that the number of filaments per fold in *C. rhizophorae*, *C. mangle*, *C. brasiliensis*, and *C. virginica* varies from 12 to 13, reaching 15 in *C. gigas*. Based on the similarity of these numbers, this parameter seems to be of little use in distinguishing the examined species. In all species of *Saccostrea* studied here, the variation is of 12–14 filaments per fold. The gills of all species in this study occupy about 1/2 of the pallial cavity area. *Saccostrea cucullata* has a medium-sized alimentary chamber, approximately 1/3 as thick as the gill fold; *S. echinata* has a thick chamber, about 1/2 as thick as the fold; *S. palmula*, *S. mordax*, and *S. glomerata* have narrow alimentary chambers, about 1/5 as thick as the gill fold.

Visceral Mass: An oyster is composed of two major interconnected subdivisions: 1) visceral mass, containing all the organ systems (digestive, excretory, reproductive), most of the muscles, and much of the nervous and circulatory systems; 2) gills and mantle/shell, which is composed of a hard portion (shell) that protects all other organs and soft parts, the mantle, which carries sensitive organs, as well as lesser parts of musculature, nervous and circulatory systems (Stenzel, 1971).

The visceral mass extends from the ventral region of the ligament to the anterior surface of the adductor muscle. It is formed by normally yellowish-colored gonads, with abundant digestive diverticula and renopericardial structures, and occupies nearly 1/4 of the total body size in all species. The gonads of all species are massive, apparently regardless of the gonadal maturation period, and surround the whole visceral mass, in some cases surrounding the region near the pyloric process. They are usually colored beige or yellowish. The genital opening has been observed in *S. cucullata* in the kidney and distinguishes itself from the surrounding area by a brownish spot.

Pericardium/Heart: The heart is located in the pericardium, a thin-walled chamber between the visceral mass and the adductor muscle. On the right side, the promial chamber extends down over the heart region and the mantle separates the pericardium wall from the shell (Galtsoff, 1964). In most Lamellibranchia, the rectum perforates the heart and passes through it, but in *Ostrea*, the heart and rectum remain apart, the heart lying beneath the rectum (Awati and Rai, 1931).

Saccostrea cucullata has a slightly enlarged ventricle with thick walls, of opaque- white color; the auricles are thin-walled and translucent and bear external sac-like structures. *Saccostrea glomerata* has a robust heart, with a relatively large ventricle, colored light cream; the auricles are elongated, robust and have the same color as the ventricle. *Saccostrea echinata* has a thin ventricle, normally translucent, and two non-pigmented auricles, both more elongated than in *S. cucullata*. The ventricle is elongated in *S. palmula*, slightly thick and whitish; the auricles are small and non-pigmented. *Saccostrea mordax* has a large ventricle, about 2/3 the size of the auricles, with whitish

coloration; the auricles are translucent and elongated. The heart size and coloration are variable in Crassostreinae.

Palps: The outline of the palps is hatchet-shaped and slightly different in each genus (Stenzel, 1971). The labial palps are large triangular flaps lying in front of the gills and attached to the visceral mass by the broad base (Awati and Rai, 1931). The palps of *Saccostrea cucullata* are large, spatuliform, have a folded anterior edge and a slightly arched ventral region. In *S. glomerata*, the palps occupy $\sim 1/5$ of the visceral mass area and are also spatuliform; their internal surface bear plicae that extend transversely to the edge. The palps of *S. echinata* are small, arched, sickle-shaped, with folds along the anterior margin. The external palps are fused in the middle, overlying the inner palps. In *S. palmula*, the palps are larger than those of the remaining species, thin, with a superior margin bearing folds. *Saccostrea mordax* has large and thick palps, with folds in the superior margin, as is the case in *S. echinata*, and the external palps overlie the inner palps for about $1/3$ of their length.

Esophagus: The mouth leads into a long esophagus; the esophagus lumen is dorsoventrally compressed and appears as a narrow slit in transverse sections. The lumen becomes narrower as it passes backward and upward to enter the dorsal region of the stomach (Awati and Rai, 1931). The esophagus is dorsoventrally compressed in all the study species; in *Saccostrea cucullata*, it is short and large, $1/2$ of palps in size; in *S. glomerata*, it is long and narrow, and also $\sim 1/2$ of palps size. In *S. echinata*, it is long and thin, and $\sim 1/3$ as long as the palps; in *S. palmula*, it is elongated and thin, and $\sim 2/3$ of palps size; in *S. mordax*, it is large and long, of same size as the palps.

Stomach: The stomach is a large sac occupying a central position in the visceral mass. This is true also for *O. edulis* (Yonge, 1926; Graham, 1949; Purchon, 1957; Reid, 1965), *C. parasitica* (Shaw and Battle, 1957) and *O. chilensis* (Purchon, 1957). Other details of the morphology and physiology of the digestive tract in Ostreidae, such as ciliary mechanisms and stomach structure and operation, can be found in the literature (Shaw and Battle, 1957; Nelson, 1960; Reid, 1965; Yonge, 1966). Internally, the study species differ in the selection area 1 (sa1), typhlosole, gastric shield, and dorsal hood. The sa1 in *Saccostrea cucullata* is short and large, with the typhlosole beginning in the posterior region of the stomach; *S. echinata* has a longer sa1, and the typhlosole begins more posteriorly than in *S. cucullata*. In *S. palmula*, the sa1 is short and narrow, with the typhlosole beginning laterally. The sa1 in *S. mordax* is long and narrow and the typhlosole is located more posteriorly than in *S. cucullata*.

The stomach has been described as bag-shaped, internally divided into a smaller anterior chamber and other larger posterior chamber, by means of a thick fold; such a fold is projected to the organ's lumen and seems to serve as a means to direct particles to the posterior region through a narrow channel (Shaw and Battle, 1957). The dorsal

hood length is nearly $1/2$ of the length of the sa1 in *S. cucullata*. In *S. mordax*, the dorsal hood has about the same length as the sa1. In *S. echinata* and *S. palmula*, the dorsal hood is short and narrow, about $1/2$ the size of those of other species.

Intestine, Rectum, Anus: The mid-gut, or intestine, originates from the stomach on the right side of the style-sac, turns around immediately to its left, and runs parallel to it all along its length; on reaching the distal end of the style-sac, the intestine turns anteriorly and runs completely back on this course (Awati and Rai, 1931). The intestine, before the style sac, passes behind the pericardium, immersed in the gonads in the visceral mass. In *Saccostrea cucullata*, *S. echinata*, *S. mordax*, and *S. glomerata*, the intestine passes behind the pericardium; in *S. palmula*, behind the esophagus. The rectum of *S. cucullata* is long and thin, surrounding the adductor muscle in $2/3$ of its concave region, with the anus bearing a single fold. *Saccostrea echinata* has a larger elongated rectum, with a shell-like anal expansion; *S. palmula* it is short and large, with the anus ending in a bell-shaped fold. *Saccostrea mordax* has a short and large rectum, and the anus bears a single fold.

In all living oysters, except for the Pycnodontinae, the rectum skirts the dorsal flank of the pericardium. In the Pycnodontinae, the rectum passes through the pericardium and the ventricle of the heart, and the anal papilla is more projected. These relative positions of the rectum and ventricle in oysters are of great taxonomic importance.

Central Nervous System: The nervous system is relatively simple, showing a pair of cerebral ganglia and a pair of visceral ganglia connected by commissures. The cerebral ganglia are somewhat inconspicuous because of their very small size and location in the visceral mass. The visceral ganglia can be easily distinguished in the anterolateral region of the adductor muscle. *Saccostrea cucullata* and *S. glomerata* have two pairs of nerves in the anterior region and three in the posterior region; *S. echinata* presents two pairs in the anterior and posterior regions; *S. mordax* and *S. palmula* have three pairs in the anterior and posterior regions.

LITERATURE CITED

- Abbott R.T. 1974. American Seashells. 2nd edition. Van Nostrand Reinhold, New York, 663 pp.
- Awati, P.R. and H.S. Rai. 1931. *Ostrea cucullata* (the Bombay oyster). Indian Zoological Memoirs 3: 1-107.
- Born, I., 1778. Index Rerum Naturalium Musei Caesarei Vindobonensis, pars prima, Testacea. Ex Officina Krausiana, Vindobonae, 442 pp.
- Born, I., 1780. Testacea Musei Caesarei Vindobonensis. Sumptibus Joannis Pauli Kraus, Vindobonae, 458 pp.
- Deshayes, G.P. 1835-1845. In: Lamarck, J.B.P.A. Histoire naturelle des animaux sans vertèbres. Deuxième édition, revue et augmentée des notes par G.P. Deshayes et H. Milne Edwards. Paris, 580 pp.

- Dillwyn L.W. 1817. A descriptive catalogue of recent shells. John & Arthur Arch, Cornhill, pp. 1–2, xii, 1–580, iv, 581–1121.
- Gmelin, J.F. 1791. Caroli a Linné Systema naturae per regna tria naturae. Editio 13, Tome 1. Pars 6. G. E. Beer, Leipzig. Pp. 3021–3910.
- Gould, A. A., 1850. Shells of the United States Exploring Expedition. Proceedings of the Boston Society of Natural History, 3: 343–348.
- Habe, T. and S. Kosuge. 1967. Shells of the World in Colour, II. The Tropical Pacific. Hoikusha, Osaka. 194 pp.
- Habe, T. and T. Okutani. 1975. Mollusca II. Gakken, Tokyo. 294 pp.
- Hanley, S. 1856. *Ostrea*. In: An Illustrated and descriptive Catalogue of recent bivalve Shells. New edition. Williams and Norgate, London, pp. 295–310.
- Harry, H.W. 1985. Synopsis of the supraspecific classification of living oysters (Bivalvia: Gryphaeidae and Ostreidae). The Veliger 28: 121–158.
- Hirase, S. 1930. On the classification of Japanese oysters. Japanese Journal of Zoology 3: 1–65.
- Huber, M. 2010. Compendium of Bivalves: a full-color guide to 3,300 of the world's marine bivalves: a status on Bivalvia after 250 years of research. Conchbooks, Hackenheim, 901 pp.
- Klinbunga, S., B. Khamnantong, N. Puanglarp, P. Jarayabhand, W. Yoosukh, and P. Menasveta. 2005. Molecular taxonomy of cupped Oysters (*Crassostrea*, *Saccostrea* and *Striostrea*) in Thailand Based on COI, 16S and 18S rDNA polymorphism. Marine Biotechnology 7: 306–317.
- Lam, K. and B. Morton 2004. The oysters of Hong Kong. (Bivalvia: Ostreidae and Gryphaeidae). The Raffles Bulletin of Zoology 52: 11–28.
- Lam, K. and Morton, B. 2006. Morphological and mitochondrial DNA analysis of the Indo-West Pacific rock oysters (Ostreidae: *Saccostrea* species). Journal of Molluscan Studies 72: 235–245.
- Lam, K. and B. Morton. 2009. Oysters (Bivalvia: Ostreidae and Gryphaeidae) recorded from Malaysia and Singapore. The Raffles Bulletin of Zoology 57: 481–494.
- Lamarck, J.B.P. de M. 1819. Histoire naturelle des animaux sans vertèbres. Suite des conchifères. Chez L'Auteur, Paris, 258 pp.
- Lamprell, K. and J. Healy. 1998. Bivalves of Australia. Vol. 2. Baekhuys Publishers, Leiden, 288 pp.
- Lamy, E. 1929. Revision des *Ostrea* vivants du Muséum National d'Histoire Naturelle de Paris. Journal de Conchyliologie 7: 1–46, 71–108, 133–168, 233–275.
- Morris, S. 1985. Preliminary guide to the oysters of Hong Kong. Asian Marine Biology 2: 119–138.
- Quoy, J.R.C. and J.P. Gaimard. 1834. Voyage de découvertes de l'Astrolabe: exécutée par ordre du Roi pendant les années 1826–1827–1828–1829, sous le commandement de M.J. Dumont D'Urville, capitaine de vaisseau. Zoologie, Tome 3, Part II. Tastu, Paris, pp. 367–954; Atlas (1834).
- Ranson, G. 1960. Les Prodissoconques (Coquilles larvaires) des Ostréides vivant. Bulletin de l'Institut Océanographique de Monaco 1183: 1–41, 136 figs.
- Ranson, G. 1967. Les especes d'huîtres vivant actuellement dans le monde, définies par leurs coquilles larvaires ou prodissoconques. Etude des collections de quelques-uns des grands musées d'histoire naturelle. Revue des Travaux de l'Institut Scientifique et Technique des Pêches Maritimes 31(2): 127–199.
- Röding, P.F. 1798. Museum Boltenianum sive Catalogus cimeliorum e tribus regnis naturae quae... Pars Secunda continens Conchylia sive Testacea univalvia, bivalvia & multivalvia. Hamburgi, Johan. Christi. Trappii, Hamburgi, pp. 1–VIII + 1–199.
- Simone, L.R.L. 1997. Anatomy and systematics of *Anodontites elongatus* (Swainson) from Amazon and Paraná basins, Brazil (Mollusca, Bivalvia, Unionoidea, Mycetopodidae). Revista Brasileira de Zoologia, Curitiba, 14: 77–888.
- Simone, L.R.L. 2009. Comparative morphology among representatives of main taxa of Scaphopoda and basal protobranch Bivalvia (Mollusca). Papéis Avulsos de Zoologia (São Paulo, 49 (32): 405–457.
- Simone, L.R.L. 2011. Phylogeny of the Caenogastropoda (Mollusca), based on comparative morphology. Arquivos de Zoologia 42 (4): 161–323.
- Smith, E.A. 1890. Report on the marine Mollusca of Ascension Island. Proceedings of the Zoological Society of London 1890(2): 317–322.
- Sowerby, G.B. 1871. Conchologia Iconica. Volume 18. *Ostrea*. L. Reeve & Co, London
- Stenzel, H.B. 1971. Oysters. In: R.C. Moore and C. Teichert (eds) Treatise on Invertebrate Paleontology. Part N: Mollusca 6, Bivalvia, vol. 3, Geological Society of America and University of Kansas Press, Lawrence, pp. N953–N1224.
- Tack, J.F., E. Vanden Berghe, and P.H. Polk. 1992. Ecomorphology of *Saccostrea cucullata* (Born, 1778) (Ostreidae) in a mangrove creek (Gazi, Kenya). Hydrobiologia 247: 109–117.
- Thomson, J.M. 1954. The genera of oysters and the Australian species. Australian Journal of Marine and Freshwater Research 5: 132–168.
- Torigoe, K. 1981. Oysters in Japan. Journal of Science, Hiroshima University, Series B, Division 1, 29: 291–481.
- Visootviseth, P.D., A. Day, and T. Siwadune. 1998. Electrophoretic and morphometric analyses in species differentiation of small oysters, *Saccostrea* spp., in Thailand. Journal of Science Society of Thailand 24: 24–36.
- Wang Y., Z. Guofan, X. Liu and X. Guo. 2008b. Classification of common oysters from north China. Journal of Shellfish Research 27: 495–503.
- Wang, H. and X. Guo. 2008a. Identification of *Crassostrea ariakensis* and related oysters by multiplex species-specific PCR. Journal of Shellfish Research 27(3): 481–487.
- Wang, Y. and X. Guo. 2008b. ITS length polymorphism in oysters and its potential use in species identification. Journal of Shellfish Research 27(3): 489–493.

A new species of *Cuthona* Alder and Hancock, 1855 (Gastropoda: Heterobranchia: Nudibranchia: Tergipedidae) from the Caribbean Sea

Ángel Valdés

Sabrina Medrano

Department of Biological Sciences
California State Polytechnic University
3801 West Temple Avenue
Pomona, CA 91768 USA
aavaldes@cpp.edu

Vishal Bhawe

Bombay Natural History Society
S.B. Singh Road, Mumbai
Maharashtra 400001, INDIA

ABSTRACT

Tergipedid nudibranch specimens from the Caribbean Sea previously identified as *Cuthona caerulea* are here described as a new species. Sequence data for the mitochondrial CO1 and 16S genes as well as the nuclear H3 are provided. A preliminary molecular phylogeny including other *Cuthona* species available in GenBank produced inconclusive results, but the new species is morphologically distinct from European specimens of *Cuthona caerulea*. Differences include radular teeth and reproductive morphology, as well as the external coloration.

INTRODUCTION

Cuthona Alder and Hancock, 1855 is a group of tergipedid nudibranchs characterized by having crowded rows of cerata, a broad foot, and arch-shaped radular teeth (Miller, 1977). Species of *Cuthona* feed on hydroids, and are most diverse in tropical and subtropical regions (Gosliner, 1981). *Cuthona* is taxonomically complex, and its taxonomic placement in relation to other genera in the Tergipedidae is controversial (Williams and Gosliner, 1979; Gosliner and Griffiths 1981; Miller, 1977; Brown, 1980; Miller, 2004).

Cuthona caerulea is a northeastern Atlantic species characterized by having a white body with numerous cerata with blue (or green) and yellow (or orange) pigment. The coloration of this species is extremely variable, but specimens with distinct color patterns are morphologically similar and regarded as members of the same species (Thompson and Brown, 1984).

Thompson and Brown (1984) reported this species for the first time from the western Atlantic, based on specimens collected from Florida, as well as records from São Paulo, Brazil (based on a personal communication by Ev. Marcus). Later, another specimen from Florida was

illustrated by Valdés et al. (2006). The western Atlantic animals display some differences in color pattern in comparison to the European ones, and some authors considered the former to belong to an undescribed species (Picton and Morrow, 1994; Calado, 2002).

In this paper we examined additional specimens recently collected in Bocas del Toro, Panama, which are externally similar to the animals illustrated from Florida by Valdés et al. (2006). These animals were found to be distinct from *C. caerulea* and are herein described as a new species.

MATERIALS AND METHODS

Specimen Collection: Four specimens were collected on unidentified hydroids at 1 m depth in Crawl Cay, Bocas del Toro, Panama, on July 30, 2015. Two specimens were preserved in ethanol 95% and two in RNAlater. The type material is deposited at the Museo de Malacología, Universidad de Panamá (MUMAUP) and the Natural History Museum of Los Angeles County (LACM).

Morphological Examination: One specimen (paratype) was dissected. The buccal mass was extracted and placed in a small glass container with NaOH 10% water solution for 60 min until the tissue was soft. The jaws were then removed and placed in ultrapure water for 5 min. The radula and remaining tissue was left for another 24 hrs. After this period, the radula was also removed from the NaOH solution and placed in ultrapure water for 5 min. The radula and jaws were mounted on a stub for scanning electron microscope (SEM) examination. The stub with the samples was coated with an Emitech K550x sputter coater at the Natural History Museum of Los Angeles County. The samples were examined under a Jeol JSM-6010 variable pressure SEM at the California State Polytechnic University.

The reproductive system was dissected from the paratype (LACM 3335), examined under a dissecting microscope (Nikon SMZ-100), and drawn with the aid of a *camera lucida* attachment. The penis was removed from the rest of the reproductive system and placed in 1 mL of hexamethyldisilazane until all the liquid evaporated. The dry and hardened penis was then mounted on a stub and sputter coated for SEM examination.

DNA Amplification and Sequencing: DNA from the paratype was sequenced for this study. DNA extractions were performed using approximately 1–3 mg of tissue taken from the foot of the animal, followed by a hot Chelex® extraction protocol with minor modifications. The tissue sample was placed into a 1.7-mL tube containing 1.0 mL TE buffer (10 mM Tris, 1 mM EDTA, pH 7.8) and incubated overnight at room temperature in a rotator. The sample was centrifuged for 3 min at 21,130 g. Subsequently, 975 µL of the original 1 mL of TE buffer was removed without disturbing the pellet of tissue. Then, 175 µL of Chelex® solution was added and heated in a 56°C water bath for 20 min and placed in a 100°C heating block for 8 min. The supernatant was the final product used for the polymerase chain reaction (PCR).

PCR was used to amplify portions of the mitochondrial cytochrome c oxidase 1 (CO1) and 16S ribosomal RNA (16S) genes, as well as the nuclear histone 3 (H3) gene. The following universal primers were used to amplify the fragments of interest: CO1 (LCO1490 5'-GGTCAACAAATCATAAAGATATTGG-3', HCO2198 5'TAAACTTCAGGGTGACCAAAAAATCA-3' developed by Folmer

et al., 1994), 16S rRNA (16S ar-L 5'-CGCCTGTTTATCAAAAACAT-3', 16S br-H 5'-CCGGTCTGAACTCAGATCACGT-3' developed by Palumbi, 1996) and H3 (H3 AF 5'-ATGGCTCGTACCAAGCAGACGGC-3', H3 AR 5'-ATATCCTTGGGCATGATGGTGAC-3' developed by Colgan et al., 1998). Confirmation of amplification was carried out using agarose gel electrophoresis with ethidium bromide to detect the presence of DNA. PCR products were sent to Source BioScience (Santa Fe Springs, California, USA) for sequencing. Sequences were assembled and edited using Geneious Pro R8 (<http://www.geneious.com>, Kearse et al. 2012). The sequences obtained were deposited in GenBank, under the accession numbers presented in Table 1.

Phylogenetic Analyses: Phylogenetic analyses were run with the new sequences obtained and a data set of other species of *Cuthona* compiled from GenBank (Table 1). Phylogenetic analyses were conducted for all genes concatenated and each gene individually. The best-fit models of evolution (GTR + G for CO1, HKY + G for 16S, HKY for H3, and GTR + I for the entire concatenated data set) were determined using the Akaike information criterion (Akaike, 1974) implemented in jModelTest (Darriba et al., 2012). A Bayesian analysis was conducted with MrBayes 3.2 (Ronquist et al., 2012), partitioned by gene (unlinked). The Markov chain Monte Carlo analysis was run with two runs of six chains for 10 million generations, with sampling every 100 generations. The default 25% burn-in was applied before constructing the majority-rule consensus tree. Convergence was confirmed by eye

Table 1. Sequences used in the phylogenetic analyses including species name, locality and GenBank accession numbers.

Species	Locality	COI	16S	H3
<i>Cuthona abronia</i>	California, USA	JQ699569	JQ699478	JQ699390
<i>Cuthona caerulea</i>	North Sea	AF249807	-	-
<i>Cuthona cocoachroma</i>	Washington, USA	GQ292071	-	-
<i>Cuthona columbiana</i>	Canada	KF643448	-	-
<i>Cuthona concinna</i>	Washington, USA	GQ292072	-	-
<i>Cuthona divae</i>	California, USA	JQ699569	JQ699479	JQ699391
<i>Cuthona fulgens</i>	California, USA	-	JQ699480	JQ699392
<i>Cuthona lagunae</i>	California, USA	-	JQ699481	JQ699393
<i>Cuthona ocellata</i>	Portugal	AY345043	-	-
<i>Cuthona sibogae</i>	-	-	GU550049	-
<i>Cuthona</i> sp. 1	Antarctica	GQ292068	-	-
<i>Cuthona</i> sp. 2	Antarctica	GQ292078	-	-
<i>Cuthona</i> sp. 3	Antarctica	GQ292066	-	-
<i>Cuthona</i> sp. 4	Antarctica	GQ292069	-	-
<i>Cuthona</i> sp. 5	Antarctica	GQ292067	-	-
<i>Cuthona</i> sp. 6	Antarctica	GQ292070	-	-
<i>Cuthona</i> sp. 7	Washington, USA	GQ292074	-	-
<i>Cuthona</i> sp. 8	Washington, USA	GQ292073	-	-
<i>Cuthona</i> sp. 9	Antarctica	GQ292075	-	-
<i>Cuthona</i> sp. 35	Philippines	JQ997026	JQ996820	JQ996921
<i>Cuthona</i> sp. PW-2014	French Polynesia	KJ522457	-	-
<i>Cuthona</i> sp. A	Philippines	JQ997019	JQ996814	JQ996913
<i>Cuthona luciae</i>	Panama	KX077954	KX077953	KX077955
<i>Tergipes tergipes</i>	Maine, USA	KJ434077	KJ434064	KJ434095

using the “Trace” function in Tracer 1.5 (Rambaut and Drummond, 2007). Maximum likelihood analyses were conducted for the entire concatenated alignment with raxmlGUI 1.0 (Silvestro and Michalak, 2012) using the bootstrap + consensus option (10,000 replicates) and the GTR + I model.

RESULTS

The Bayesian consensus tree was relatively well-resolved, but most nodes were not supported in the maximum likelihood tree (Figure 1). Only two clades, one including *Cuthona fulgens* (MacFarland, 1966) from California and two unidentified species from Washington and the Philippines, and another including *Cuthona divae* (Er. Marcus, 1961) and *Cuthona concinna* (Alder and Hancock, 1843), are well supported. Additionally, the phylogenetic position of the specimens from Panama, sequenced here in relation to a specimen of *Cuthona caerulea* from Europe, was not resolved.

Anatomical data revealed consistent differences between Panamanian and European specimens. Therefore, the taxon from Panama is below described as a new species.

The morphological differences are described in the Discussion section.

SYSTEMATICS

Tergipedidae Bergh, 1889

Cuthona luciae new species

(Figures 2–11)

Cuthona caerulea (non Montagu, 1804).—Thompson and Brown, 1984: 121; Valdés et al. 2006: 264, 265

External Morphology: Live animals up to 12 mm length. Body narrow, elongated (Figure 2). Cerata elongated, cylindrical, dorso-lateral, arranged in 13–14 vertical rows, with 4–5 cerata in each row. Oral tentacles smooth. Rhinophores smooth, similar in length to oral tentacles. Reproductive opening located on right side of body, between first and second groups of cerata. Anus acleiproctic, dorso-lateral, posterior to pericardium. Body background color gray with irregular yellow spots. Posterior of dorsum dark blue. Dense yellow spotting on pericardium, behind second row of cerata. Rhinophores

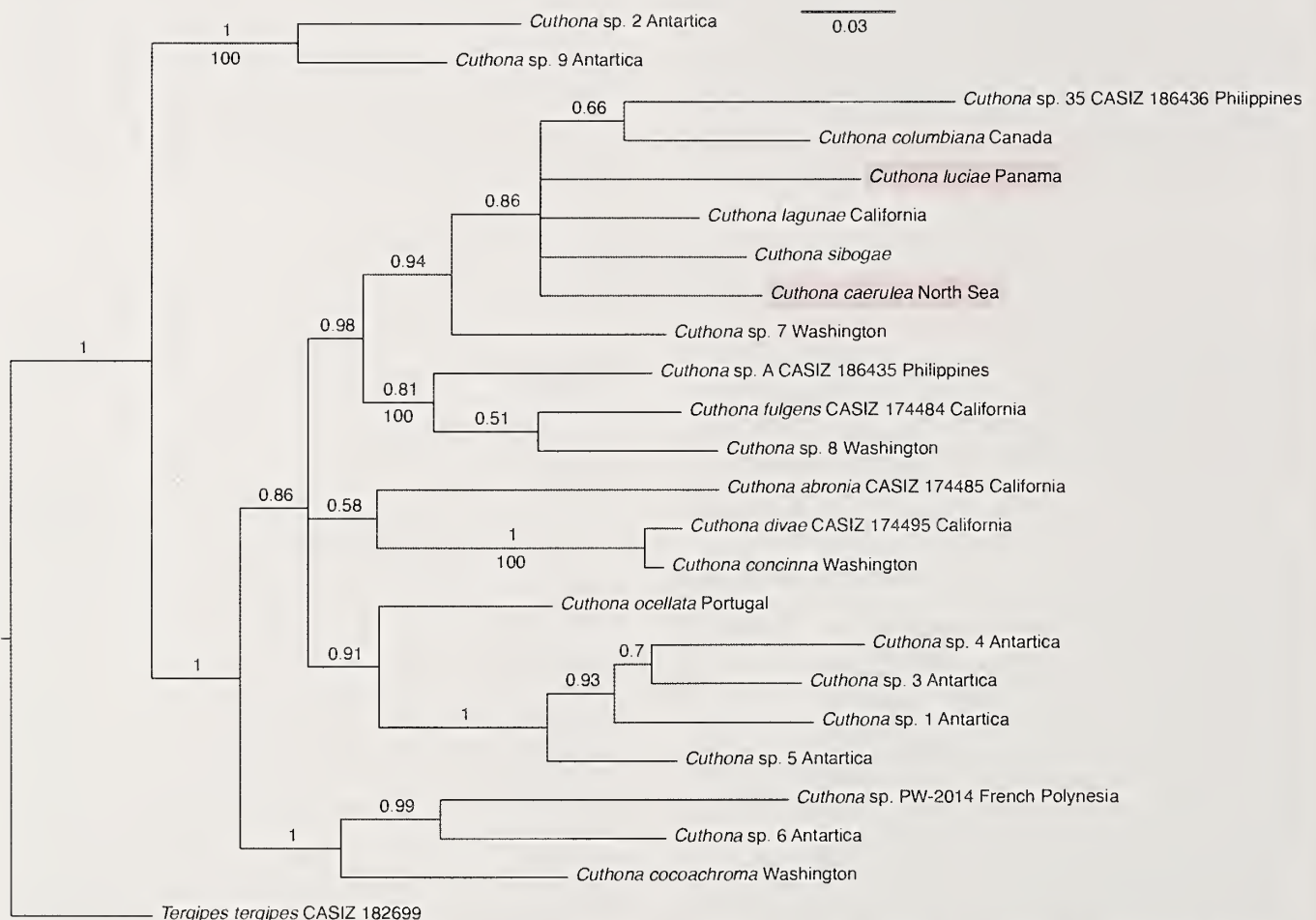
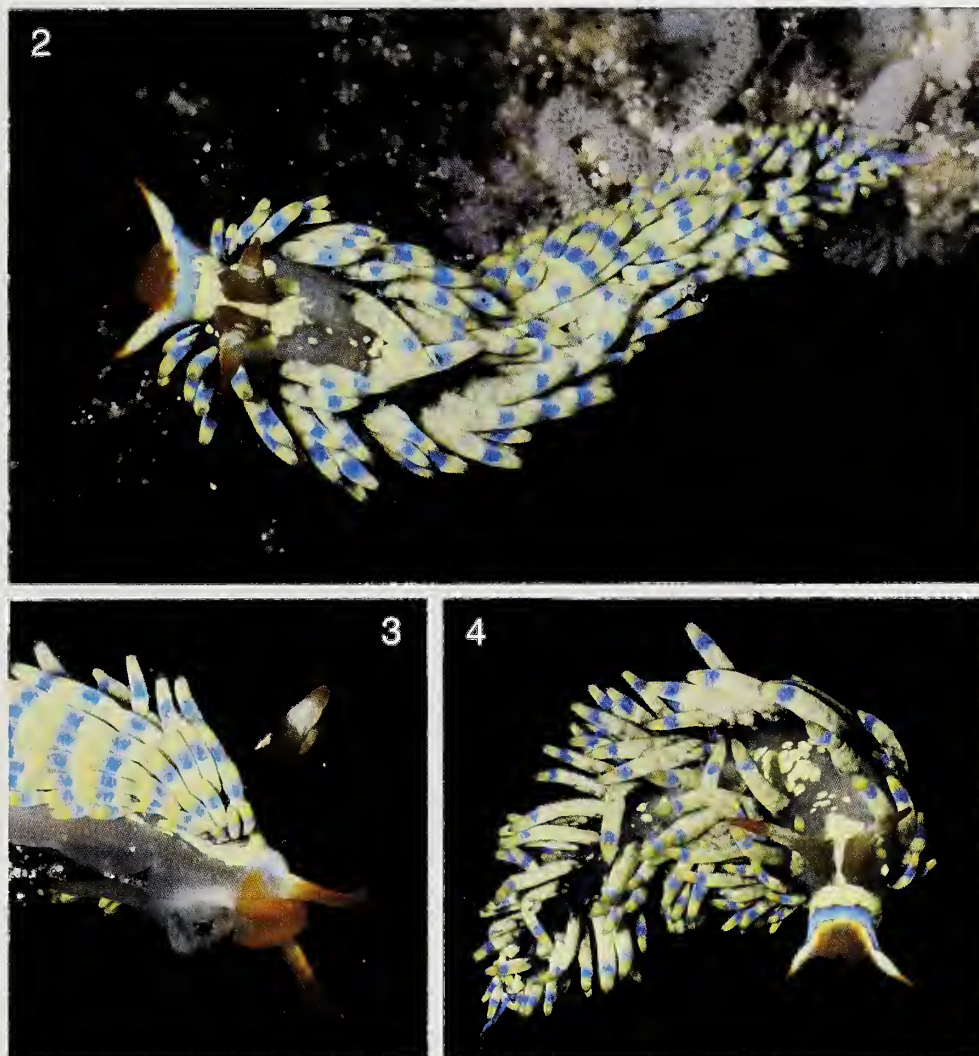


Figure 1. *Cuthona*. Bayesian consensus tree of the concatenated analysis including posterior probabilities and bootstrap values from the maximum-likelihood analysis.



Figures 2–4. *Cuthona luciae* new species. Photographs of live holotype (MUMAUP MOL-GAS-001). 2. Dorsal view of animal on its hydroid prey, with egg mass visible. 3. Lateral view of head. 4. Dorsal view on black background.

opaque gray with white mid-region and orange apices. Yellow pigment on head, surrounding base of rhinophores. Cerata opaque yellow with blue band toward distal end before reverting to yellow. Oral tentacles opaque yellow with dark orange tips. Blue transverse band connecting bases of oral tentacles. Anterior end of head dark orange.

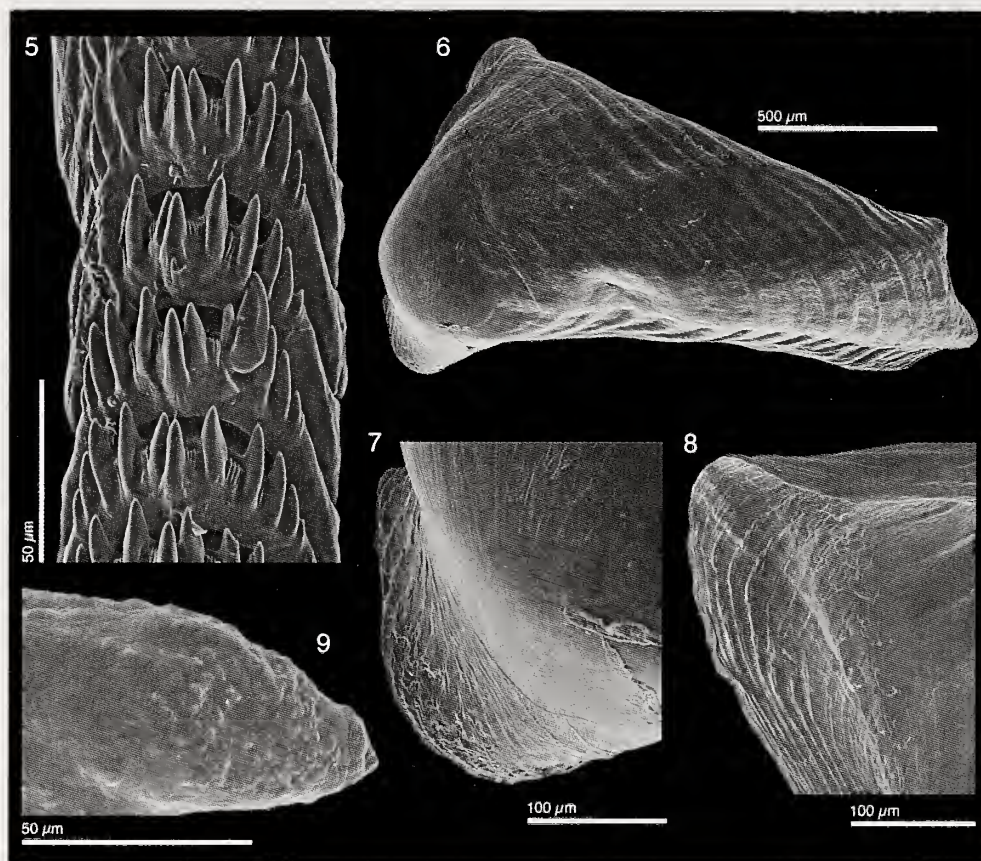
Anatomy: Radular formula $68 \times 0.1.0$ in 12 mm preserved length paratype (LACM 3335). Radular teeth with 9–10 large, sharp denticles, which decrease in size toward lateral sides of teeth and again toward center (Figure 5). Denticles separated by gaps, which become wider towards center of teeth. Gaps filled with tiny, sharp denticles, which vary in number depending on width of gap and are absent from most lateral gaps. Cusp about same length, or shorter, than central denticles, and only distinguishable from denticles because it emerges from slightly higher plane. Jaws elongate (Figure 6) with smooth masticatory borders (Figures 7–8).

Reproductive system (Figure 10) with an elongate ampulla connecting directly into female gland complex. Prostate emerges from female gland complex, near insertion point of ampulla. Prostate long and convoluted, narrowing abruptly at distal end, to expand again into deferent duct. Distal portion of deferent duct containing large penis with apical stylet (Figures 9, 11). Vagina slightly curved, connecting directly into rounded bursa copulatrix.

Type Material: HOLOTYPE: MUMAUP MOL-GAS-001, July 30, 2015; PARATYPE: LACM 3335, July 30, 2015; all from type locality.

Type Locality: Crawl Cay, Bocas del Toro, Panama.

Geographic Range: Florida (Thompson and Brown 1984, Valdés et al. 2006) to Panama (present paper) and possibly Brazil (Thompson and Brown 1984).



Figures 5–9. *Cuthona luciae* new species. Scanning electron micrographs of radular teeth, jaws, and penis of paratype (LACM 3335). 5. Radular teeth. 6. Jaw. 7. Dorsal view of the masticatory border. 8. Ventral view of the masticatory border. 9. Penis.

Etymology: Named after Lucía Valdés, daughter of the senior author.

DISCUSSION

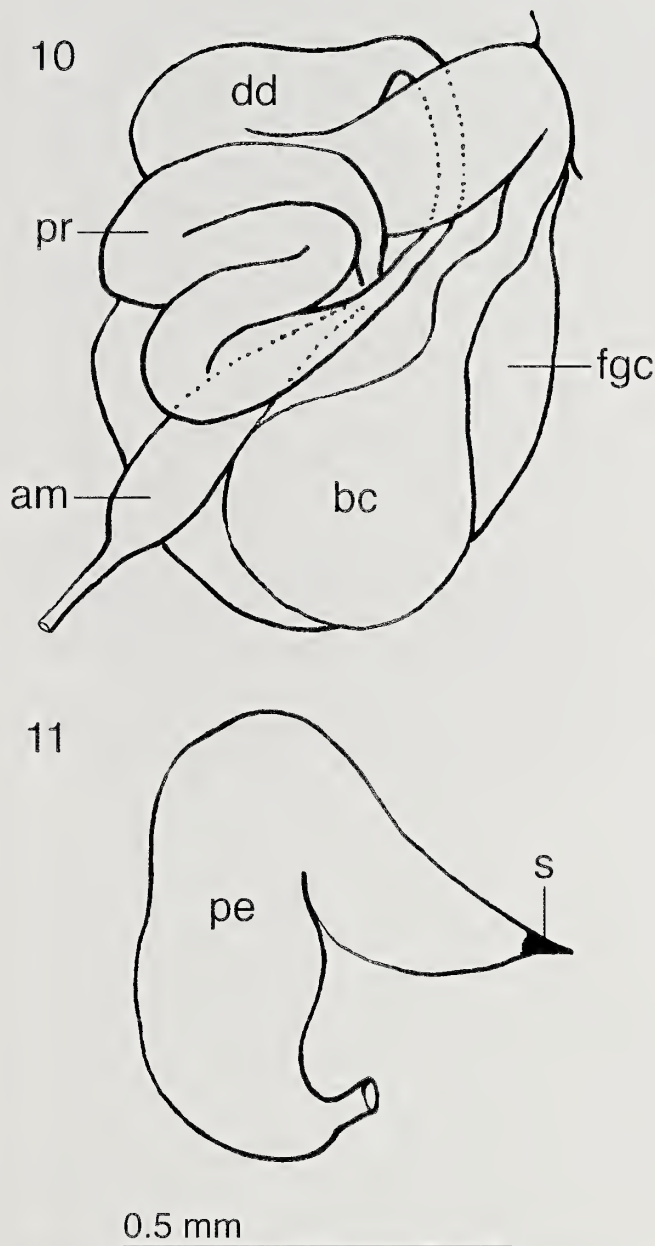
The phylogenetic analyses resulted in poorly supported trees. Although the Bayesian consensus tree contains well-supported nodes, many of those are not supported in the maximum likelihood consensus tree. This study has not produced a reliable phylogeny for the species of *Cuthona* sequenced to date. The results of this phylogenetic analysis are also inconclusive as to the position of the species here described relative to a European specimen of *Cuthona caerulea*. However, a Bast-n search in GenBank revealed that the COI sequence of *C. caerulea* from the North Sea in GenBank (AF249807) and the sequence from *C. luciae* are only 82% identical, which is consistent with species-level differences. In addition, the morphological examinations revealed the presence of several unique characteristics that support that the Caribbean animals constitute a distinct species.

The radular teeth of *Cuthona luciae* are very different from those of *C. caerulea* described from European specimens. Schmekel and Portman (1982) illustrated three radular teeth in lateral view of a specimen collected in

Naples, Italy. These teeth had 6 lateral denticles of similar size and a larger central cusp. Thompson and Brown (1984) illustrated one radular tooth of a specimen from Lundy, England, which had 5 lateral denticles, but was otherwise similar to the Mediterranean radula illustrated by Schmekel and Portman (1982). These radulae are very different from the Caribbean specimens here examined, in which the teeth contain denticles separated by gaps filled with tiny, sharp denticles, varying in number depending on the width of the gap. Additionally, the jaws of European specimens have a distinct masticatory border with denticles (Thompson and Brown, 1984), which is absent in the Caribbean animals, although Schmekel and Portman (1982) reported that it can be absent in Mediterranean specimens as well.

Schmekel and Portman (1982) illustrated the reproductive system of a specimen from Naples, Italy. Although the reproductive system of the specimen examined from the Caribbean is similar, there are two fundamental differences, the European specimens have a well-formed penial gland, absent in the Caribbean animal; in addition, the Caribbean animal has a penial stylet, which is not reported in the European specimen.

A similar species to *Cuthona luciae* is *Cuthona herrerae* Ortea, Moro, and Caballer, 2001, originally described from Cape Verde, Eastern Atlantic. The radular teeth of



Figures 10, 11. *Cuthona luciae* new species. Reproductive system of paratype (LACM 3335). **10.** Dorsal view of the reproductive system. **11.** Detail of the penis. Abbreviations: **am**, ampulla; **bc**, bursa copulatrix; **dd**, deferent duct; **fgc**, female gland complex; **pe**, penis; **pr**, prostate; **s**, penial stylet.

C. herrerae are very similar to those of *C. luciae* in having large denticles separated by gaps containing tiny denticles (Ortea et al. 2001). However, many other characteristics differentiate these two species, for example the jaws of *C. herrerae* contain denticles on the masticatory border, absent in *C. luciae*; *C. herrerae* has less rows of cerata and less cerata per row than *C. luciae*; more importantly, *C. herrerae* lacks orange pigment on the oral tentacles and the characteristic bright blue band on the head of *C. luciae*. Although the cerata

of the two species bear similar colors, they are much brighter in *C. luciae*.

Also, *Cuthona iris* Edmunds and Just, 1983, originally described from Barbados, has a similar color pattern with yellow cerata, each with a blue band (see Valdés et al. [2006] for a color illustration). But the body of this species is predominantly yellow, including the rhinophores and oral tentacles, it has a light blue dorsal band, absent in *C. luciae*, and lacks the characteristic head pigmentation of *C. luciae*.

Although morphological evidence confirmed that *Cuthona luciae* is distinct from *C. caeurela* and other similar species such as *C. herrerae* and *C. iris*, further research is necessary to determine the phylogenetic position of *C. luciae* and to resolve the evolutionary relationships within Tergipedidae. The sequence data provided here should facilitate future work toward these goals.

ACKNOWLEDGMENTS

The SEM work was conducted at the California State Polytechnic University SEM laboratory supported by the US National Science Foundation (NSF) grant DMR-1429674. The fieldwork in Panama was conducted during the course "Taxonomy and Biology of Sea slugs" funded by awards NSF DEB-1355190 and DEB-1355177, and organized by Rachel Collin of the Smithsonian Tropical Research Institute in Bocas del Toro. The travel expenses of AV and SB were also supported by the NSF, and those of VB by the British Ecological Society (travel grant 5585-6629), and the Bombay Natural History Society. Several staff members of the Smithsonian Tropical Research Institute in Bocas del Toro facilitated the fieldwork activities: Plinio Gondola, Urania Gonzalez, Tanyusha Grenald, Arcadio Castillo, Deyvis Gonzalez, and Nerea Nieto. Collecting of specimens was possible with permits ARAP 27 (2015) and ANAM SE/A-64-15 issued by the Panamanian Government.

LITERATURE CITED

- Akaike, H. 1974. A new look at the statistical model identifications. *IEEE Transactions on Automatic Control* 19: 716–723.
- Brown, G.H. 1980. The British species of the aeolidacean family Tergipedidae (Gastropoda: Opisthobranchia) with a discussion of the genera. *Zoological Journal of the Linnean Society* 69: 225–255.
- Calado, G. 2002. New records for the Azorean opisthobranch fauna (Mollusca: Gastropoda). *Arquipélago, Life and Marine Sciences* 19A: 103–106.
- Colgan, D.J., A. Mclauchlan, G.D.F. Wilson, S.P. Livingston, G.D. Edgecombe, J. Macaranas, G. Cassis, and M.R. Gray. 1998. Histone H3 and U2 snRNA DNA sequences and arthropod molecular evolution. *Australian Journal of Zoology* 46: 419–437.
- Darriba, D., G.L. Taboada, R. Doallo, D. Posada. 2012. jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods* 9: 772.

- Folmer, O., M. Black, W. Hoeh, R. Lutz, and R. Vrijenhoek. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.
- Gosliner, T.M. 1981. A new species of tergipedid nudibranch from the coast of California. *Journal of Molluscan Studies* 47: 200–205.
- Gosliner, T.M. and R.J. Griffiths. 1981. Description and revision of some South African aeolidacean Nudibranchia (Mollusca, Gastropoda). *Annals of the South African Museum* 84: 105–150.
- Kearse, M., R. Moir, A. Wilson, S. Stones-Havas, M. Cheung, S. Sturrock, S. Buxton, A. Cooper, S. Markowitz, C. Duran, T. Thierer, B. Ashton, P. Mentjies, and A. Drummond. 2012. Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28: 1647–1649.
- Miller, M.C. 1977. Aeolid nudibranchs (Gastropoda: Opisthobranchia) of the family Tergipedidae from New Zealand waters. *Zoological Journal of the Linnean Society* 60: 197–222.
- Miller, M.C. 2004. An appraisal of the identity of the New Zealand species of the aeolid nudibranch family Tergipedidae (Gastropoda: Opisthobranchia). *Journal of Natural History* 38: 1183–1192.
- Palumbi, S.R. 1996. Nucleic acids II: The polymerase chain reaction. In: D.M. Hillis, C. Moritz, and B.K. Mable (eds.) *Molecular Systematics*, 2nd Edition. Sinauer, Sunderland, Massachusetts, pp. 205–247.
- Picton, B.E. and C.C. Morrow. 1994. *A Field Guide to the Nudibranchs of the British Isles*. Immel Publishing Limited, London, 143 pp.
- Rambaut, A. and A.J. Drummond. 2007. Tracer v1.4. Available at <http://tree.bio.ed.ac.uk/software/tracer/>
- Ronquist, F., M. Teslenko, P. van der Mark, D.L. Ayres, A. Darling, S. Höhna, B. Larget, L. Liu, M. A. Suchard, and J.P. Huelsenbeck. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542.
- Schmekel, L. and A. Portmann. 1982. *Opisthobranchia des Mittelmeeres. Nudibranchia und Sacoglossa*. Springer-Verlag, Berlin, 410 pp.
- Silvestro, D. and I. Michalak. 2012. RaxmlGUI: A graphical front-end for RAxML. *Organisms Diversity and Evolution* 12: 335–337.
- Thompson, T.E. and G.H. Brown. 1984. *Biology of Opisthobranch Molluscs*, Volume 2. Ray Society, London, 229 pp.
- Valdés, A., J. Hamann, D.W. Behrens, and A. DuPont. 2006. *Caribbean Sea Slugs: A Field Guide to the Opisthobranch Mollusks from the Tropical Northwestern Atlantic*. Sea Challengers Natural History Books, etc, Gig Harbor, Washington, 289 pp.
- Williams, G.C. and T.M. Gosliner. 1979. Two new species of nudibranchiate molluscs from the west coast of North America, with a revision of the family Cuthonidae. *Zoological Journal of the Linnean Society* 67: 203–223.

The genera *Miraclathurella* Woodring, 1928 (Gastropoda: Pseudomelatomidae) and *Darrylia* García, 2008 (Gastropoda: ?Horaiclavidae), with two proposed new combinations for *Darrylia*

Emilio F. García

115 Oak Crest Dr.
Lafayette, LA 70503
Efg2112@louisiana.edu

ABSTRACT

The genera *Miraclathurella* Woodring, 1928 and *Darrylia* García, 2008 are compared. *Miraclathurella clendenini* and *M. peggywilliamsae* are reassigned to *Darrylia*.

INTRODUCTION

Miraclathurella Woodring, 1928 and *Darrylia* García, 2008 are two genera that are similar in conchological characters. However, Bouchet et al. (2011) have placed *Miraclathurella* in the family Pseudomelatomidae and tentatively placed *Darrylia* in the recently erected family Horaiclavidae. According to Bouchet et al. (2011: 293), the family Horaiclavidae “shares many characters with Pseudomelatomidae, conchologically differing by a small stout shell with short siphonal canal and usually poorly developed spiral sculpture”. Puillandre et al. (2001) further define Horaiclavidae, stating that it “mostly includes genera previously placed in the Drilliidae and Pseudomelatomidae.” Molecular data clearly show that the included genera are distinct in these families and correspond to a highly supported clade, currently arranged as a sister clade to the Clavatulidae (Puillandre, 2011: 269). Unfortunately, molecular data has not been available for either *Miraclathurella* or *Darrylia*.

The genus *Miraclathurella* was proposed by Woodring (1928: 191) to accommodate turrid-like mollusks with, among other characters, a stout, broad-tipped nucleus “consisting between two and a half and three whorls, the end of the last whorl bearing a few coarse curved, protractive axial riblets.” The aperture is “very long and narrow”, and the anterior canal “relatively long.” Woodring named two species in *Miraclathurella*: *M. vittata* (Figure 1), with a protoconch of “about three whorls, about the last half whorl bearing an anterior keel, behind which lie axial riblets,” and *M. entemna* (Figure 2), with a protoconch “consisting of about two and a half whorls, the last quarter

whorl bearing an obscure anterior keel, behind which lie a few obscure axial riblets.” Although Woodring considered the Bowden beds to be of Miocene origin, studies of the foraminifers in the area have proved them to be younger, from the Pliocene Epoch (Donovan, 1998).

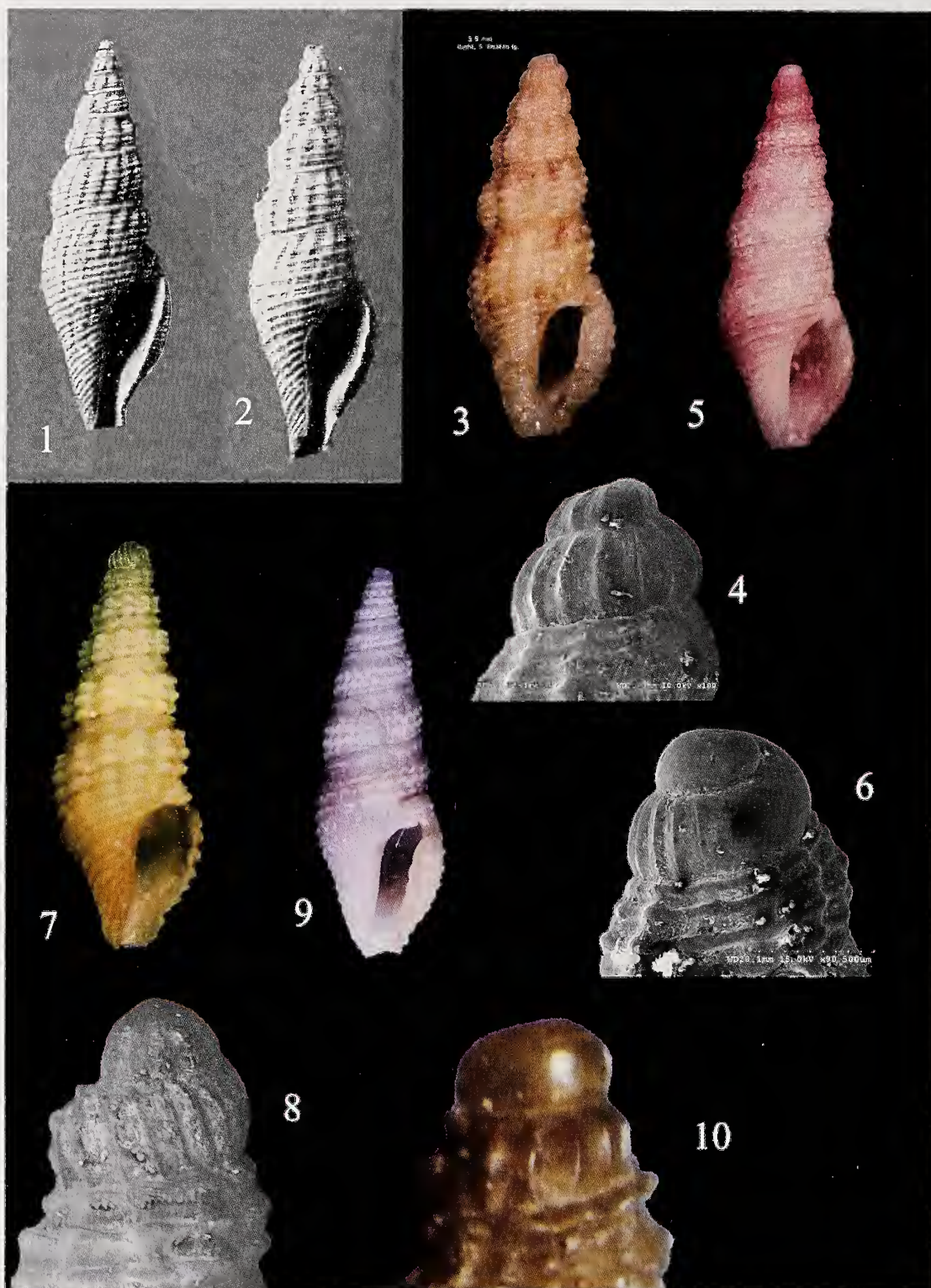
Use of the genus *Miraclathurella* remained restricted to fossil species from Bowden described by Woodring until 1971, when Shasky described *Miraclathurella mendozana* from the recent fauna of the Panamic Province. In his Discussion (Shasky, 1971: 68), that author compared this species to *Clathrodrillia woodringi* Pilsbry and Olsson, 1941, a species described as a Pliocene fossil from the Canoa Formation of Ecuador, which Shasky also assigned to *Miraclathurella*. Also in 1971, Keen transferred *Pleurotoma bicanalifera* Sowerby, 1934 to *Miraclathurella* (Keen, 1971: 728, fig. 1719).

The genus *Miraclathurella* did not appear in the literature of the recent fauna of the western Atlantic until 1988, when Jong and Coomans (1988) transferred *Drillia kleinrosa* Nowell-Usticke, 1969, from the shallow waters around Aruba, Bonaire and Curaçao, to *Miraclathurella*. And two decades later a second species, *M. clendenini* García, 2008, from Bahía de Campeche, was tentatively placed in that genus. A third species, *M. peggywilliamsae* Fallon, 2010, from St. Vincent and the Grenadines soon followed.

Although Jong and Coomans placed *kleinrosa* in *Miraclathurella*, the species did not seem to fit Woodring’s description of that genus, lacking any vestige of a keel on the protoconch and possessing a short, not long, siphonal canal so when a second species with the same differentiating characters was discovered in Roatán Island, Honduras, there seemed to be a need to create a taxon that would include those two species, and the genus *Darrylia* was proposed.

DISCUSSION

Darrylia differs from *Miraclathurella* in having more solid, more stout shells; a paucispiral nucleus of less than two whorls that are almost completely, or partially, axially ribbed; a short aperture which occupies no more than



Figures 1–10. Species of *Miraclathurella* and *Darrylia*. **1.** *Miraclathurella vittata* Woodring, 1928, Holotype, USNM 135376, length 12 mm, width 4 mm, Bowden Formation, Jamaica. **2.** *Miraclathurella entemna* Woodring, 1928, Holotype, USNM 135374, length 15.5 mm, width 4.7 mm, Bowden Formation, Jamaica. **3, 4.** *Darrylia harryleei* García, 2008, Holotype, ANSP 416409, length 5.9 mm, width 2.1 mm, Oakridge, Roatán I., Honduras, 0.2 m depth. **5, 6.** *Darrylia kleinrosa* (Nowell-Usticke, 1969), EFG 13924, length 6.5 mm, off Hotel Bonaire, Bonaire I., Netherlands Antilles, 2.5–3.0 m depth. **7, 8.** *Darrylia clendenini* (García, 2008), Holotype ANSP 416411, length 8.2 mm, width 3.2 mm, Bahía de Campeche, southwestern Gulf of Mexico, 20°51.49' N, 92°21.44' W, 63–65 m depth. **9, 10.** *Darrylia peggywilliamsae* (Fallon, 2010), Holotype USNM 1139716, length 10.3 mm, width 3.6 mm, Baliceaux Island, St. Vincent and the Grenadines, Caribbean Sea.

one third the length of the shell; and a truncated shell with a shorter anterior canal. When the genus *Darrylia* was proposed, only *D. harryleei* (Figures 3, 4) and *D. kleinrosa* (Figures 5, 6) were considered. Despite its obvious similarities with *Darrylia*, the species *clendenini* (Figures 7–8) was tentatively placed in *Miraclathurella* mainly because of the presence of (1) a subsutural cord and (2) a somewhat longer anterior canal. However, the discovery of “*Miraclathurella*” *peggywilliamsae* (Figures 9–10), which also has a subsutural cord, and which otherwise fits well in *Darrylia*, has led me to conclude that some members of the genus *Darrylia* do possess a subsutural cord. One may point out that the almost completely ribbed protoconch of *D. clendenini* (Figure 4) does compare well with that of *D. harryleei* (Figure 8), the type species of *Darrylia*; and that the first smooth, then ribbed protoconch of *D. peggywilliamsae* (Figure 10) reflects the characters of the protoconch of *D. kleinrosa* (Figure 6).

Comparing the plate images of *Miraclathurella* spp. (Figures 1–2) and *Darrylia* spp. (Figures 3, 5, 7, 9) they illustrate the differences between the two genera. *Darrylia clendenini* still seems to show a somewhat more elongated anterior canal, but the specimen figured, as well as all other specimens from the type material, were sub-adult, and the outer lip had not yet thickened, which gives it that seemingly uncharacteristic appearance.

Drawing from the considerations above, I propose that *Miraclathurella clendenini* García, 2008 and *M. peggywilliamsae* Fallon, 2010 be assigned to *Darrylia*.

Two recent species from the Panamic Province have been placed in *Miraclathurella*. However, Keen's new combination of *M. bicanalifera* is believed to be in error, as the species characters are more similar to those of *Glyphostoma*. *Glyphostoma epicasta* Bartsch, 1934 is its western Atlantic cognate. Compare Keen (1971:726, fig. 11) with Bartsch (1934, pl. 4, figures 4, 7, 9), and with the figure at <http://www.jaxshells.org/glypepicj.htm>.

The multispiral protoconchs in *Miraclathurella* species indicate planktotrophic larval development and resulting broader distributions for these species. This could explain the presence of a broadly distributed ancestor to both the new species and the recent eastern Pacific species *M. mendozana*. Although Shasky described the protoconch as “smooth” (Shasky, 1971: 68), without the axial riblets described by Woodring, the shell does have all the other characters of *Miraclathurella*.

In the western Atlantic, the genus *Miraclathurella* seems to be restricted to the Pliocene beds at Bowden, Jamaica. The genus *Darrylia*, characterized by a paucispiral protoconch, has so far produced four distinct populations: *Darrylia peggywilliamsae* in the St. Vincent

Grenadines area in the southeastern Caribbean, *D. kleinrosa* around the ABC islands, Netherlands Antilles, in the southwestern Caribbean, *D. harryleei* in the Bay Islands, Honduras, and *D. clendenini*, in the southwestern Gulf of Mexico.

ACKNOWLEDGMENTS

My thanks to Phillip Fallon for allowing me to reproduce the images of the holotype of *Miraclathurella peggywilliamsae*; he has also critically read the ms, providing information that improved the quality of the paper. The figures of *Miraclathurella vittata* and *M. entemna* are reproduced from Woodring (1928: pl. 8, figures 2 and 5).

LITERATURE CITED

- Bartsch, P. 1934. Reports on the collections obtained by the first Johnson-Smithsonian Deep-sea Expedition to the Puerto Rican Deep. New mollusks of the family Turritidae. Smithsonian Miscellaneous Collections 91(2): 1–29, 8 pls.
- Bouchet, P., Yu. I. Kantor, A. Sysoev, and N. Puillandre. 2011. A new operational classification of the Conoidea. Journal of Molluscan Studies 77: 273–308.
- Donovan, S.K. 1998. An introduction to the Bowden Shell Bed, Southeast Jamaica. Contributions to Tertiary and Quaternary Geology 35: 3–8, 4 figs.
- Fallon P.J. 2010. Descriptions and illustrations of some new and poorly known turrids of the tropical northwestern Atlantic. Part I. Genera *Buchema* Corea, 1934 and *Miraclathurella* Woodring, 1928 (Gastropoda: Turridae: Crassispirinae). The Nautilus 124: 166–174.
- García, E.F. 2008. Eight new molluscan species (Gastropoda: Turridae) from the western Atlantic, with the description of two new genera. Novapex 9: 1–15.
- Jong, K.M. de and H.E. Coomans. 1988. Marine gastropods from Curaçao, Aruba and Bonaire. Studies on the Fauna of Curaçao and other Caribbean Islands 69: 1–261, 47 pls.
- Pilsbry, H.A. and A.A. Olsson. 1941. A Pliocene fauna from western Ecuador. Proceedings of the Academy of Natural Sciences of Philadelphia 93: 1–79, pls. 1–19.
- Puillandre, N., Yu. I. Kantor, A. Sysoev, A. Couloux, C. Meyer, T. Rawlings, J.A. Todd and P. Bouchet. 2001. The dragon tamed? A molecular phylogeny of the Conoidea. Journal of Molluscan Studies 77: 259–272.
- Shasky, D.R. 1971. Ten new species of tropical eastern Pacific Turridae. Veliger 14: 67–72.
- Nowell-Usticke, G.W. 1969. A Supplementary Listing of New Shells, to be added to the Check List of the Marine Shells of St. Croix. Author edition, St. Croix, 32 pp., 6 pls.
- Woodring, W.P. 1928. Miocene Mollusks from Bowden, Jamaica. Part II. Gastropods and discussion of results. Carnegie Institute of Washington Publication 385, vii + 564 pp., 40 pls.

Sponsored in part by the State of
Florida, Department of State,
Division of Cultural Affairs and the
Florida Council on Arts and Culture



INSTRUCTIONS TO AUTHORS

THE NAUTILUS publishes articles on all aspects of the biology, paleontology, and systematics of mollusks. Manuscripts describing original, unpublished research and review articles will be considered. Brief articles, not exceeding 1000 words, will be published as notes and do not require an abstract. Notices of interest to the malacological community will appear in a notices section.

Manuscripts: Each original manuscript and accompanying illustrations should be submitted to the editor preferably via e-mail or as hardcopy in triplicate.

Text must conform to the dimensions of $8\frac{1}{2} \times 11$ -inch paper, double-spaced, and single-column throughout (including literature cited, tables, and figure captions). Authors should follow the general recommendations of *Scientific Style and Format—The CSE Manual for Authors, Editors, and Publishers*, available from the Council of Science Editors at www.councilscienceeditors.org. The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Metric, not English, units are to be used. Geochronologic modifiers should be capitalized only when units are formally recognized: for instance, use Late Cretaceous but early Miocene. Likewise, only modifiers of formally recognized chronostratigraphic units are capitalized: use Lower Jurassic but upper Oligocene.

The sequence of sections should be title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, tables, figure captions, figures. The title page should include the title, author's name(s) and address(es). If corresponding author is not the senior author, please indicate. The abstract should summarize in 250 words or less the scope, main results, and conclusions of the article. Abstracts should be followed by a list of additional key words. All references cited in the text must appear in the Literature Cited section and vice-versa. Please follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included within the pagination of cited work. Tables must be numbered and each placed on a separate page. If in doubt, please follow a recent issue of the journal for sequence of sections and other style requirements.

Illustrations: Illustrations are rendered either at full-page width (maximum width 17 cm) or column width (maximum width 8.2 cm). Please take these dimensions into consideration when preparing illustrations. Page-width illustrations ideally should span the entire width of printed page (17 cm). "Tall" page-width illustrations should be avoided, square or "landscape" formats work better. Please design plates accordingly, such that there will be enough space left at the bottom of printed page for plate caption. (Digital technology has made this task much easier.)

All line drawings must be in black, clearly detailed, and completely labeled. Abbreviation definitions must be included in the caption. Line drawings must be high resolution files at least 600 dpi (dots per inch) resolution at actual size. Standard digital formats for line drawings include .tif, .bmp, .psd, .eps, and .pdf.

Photographs may be submitted in black-and-white or color, preferably in RGB mode if in color. Standard digital formats for photographs include .tif, .psd, .jpg, or .pdf. Photographs must be high resolution files at least 300 dpi resolution at actual size.

If more than one figure is included in an illustration, all figures are to be consecutively numbered (Figures 1, 2, 3, . . . , NOT Figures 1A, 1B, 1C, . . . , NOR Plate 1, Figure 1, . . .). In illustrations with more than one figure, make sure that blank areas between figures is kept to a minimum, thereby allowing for more area for each individual figure.

Compressed files (e.g., .jpg) may be used to facilitate transmission of files during original submission, but may not be acceptable at final submission (see below).

Voucher Specimens: Deposition of the holotype in a recognized institutional, public collection is a requirement for publication of articles in which new species-level taxa are described. Deposition of paratypes in institutional collections is strongly encouraged, as is the deposition of representative voucher specimens for all other types of research work.

The Editorial Process: Upon receipt, all manuscripts are assigned a number and acknowledged. The editor reserves the right to return manuscripts that are substandard or not appropriate in scope for THE NAUTILUS. Manuscripts deemed appropriate for the journal will be sent for critical review to at least two reviewers. The reviewers' recommendations will serve as basis for rejection or continuation of the editorial process. Reviewed manuscripts will be sent back to authors for consideration of the reviewers' comments. The revised version of the manuscript may at this point be considered accepted for publication by the journal.

Final Submission: Authors of accepted manuscripts are required to submit a final version via e-mail to the editor at jleal@shellmuseum.org. Please do not send low-resolution or compressed illustration files at this stage. Send any files larger than 20 Mb on a CD or DVD to the editor.

Proofs: After typesetting, proofs will be sent to the author. Author should read proofs carefully and send corrections to the editor within 48 hours. Changes other than typesetting errors will be charged to the author at cost.

Offprints: An order form for offprints will accompany the proofs. Offprints will be ordered through the editor. Authors with institutional, grant, or other research support will be asked to pay for page charges at the rate of \$60 per page.

SMITHSONIAN LIBRARIES



3 9088 01925 6817